Succession of Collembola in the post-mining landscape of Lower Lusatia

Von der Fakultät für Umweltwissenschaften und Verfahrenstechnik der Brandenburgischen Technischen Universität Cottbus zur Erlangung des akademischen Grades eines Doktor der Naturwissenschaften genehmigte Dissertation

vorgelegt von

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“The great tragedy of Science – the slaying of a beautiful hypothesis by an ugly fact.”

T. H. Huxley

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1. Introduction

Among the various types of succession (e.g. BURROWS 1990, TOWNSEND et al. 2000, BEGON et al. 2002), primary or autogenic succession has been regarded from the very beginning of succession research (CLEMENTS 1916) as the most interesting one (WIEGLEB & FELINKS 2001b). In primary succession, community processes can be studied disregarding historical effects and continuous anthropogenetic disturbance. Thus, the probability of discovering general ecological principles in primary succession studies can be regarded as high (WIEGLEB & FELINKS 2001b). Primary succession on a landscape scale is caused by a catastrophic event which leaves or creates an area without organisms or biotic soil structure (DUNGER & WANNER 1999, TOWNSEND ET AL. 2000, BEGON 2002). In Lower Lusatia this was caused by the removal of the overlying rock, removal of the lignite seams and dumping of mingled tertiary and quaternary substrates.

In a wider sense, succession can be regarded as the sequential (or directional) change of species number, species composition and community structure, including dominance relations and community type in a site (DIERSCHKE 1994, BRÖRING & WIEGLEB 1998, BLUMRICH et al. 1998, BEGON et al. 2002). DUNGER & WANNER (1999) define succession in an ecosystem as a temporarily limited process which is irreversible and leads to a constant increase in diversity, structure and biomass. The first contact of lithosphere and biosphere would be the beginning of succession. From that point on, the sterile soil can be colonized by air (aptertion). However, the strict concept of linear succession in post-mining areas is rejected by FELINKS (2000), who describes explicitly succession of flora with stages of stochastic regression and rather web-like stages of succession.

BEGON et al. (2002) describe succession as directional continuous pattern of colonisation and extinction by species populations. This phenomenon was much earlier described by THOREAU (1899) and CLEMENTS (1916). View was concentrated on models of “plant by plant replacement” (CONNELL & SLATYER 1977, NOBLE 1981, WHELAN 1989). The relevance of animals in succession was often considered as of minor importance (BRADSHAW 1983), although the theory of ODUM (1953, 1969) already bases on a concept of ecosystems. The actual relevance of fauna in succession was recognized later (SCHWERDTFEGER 1975, MAJER 1989).

Primary succession in the post-mining landscape (PML) however is distinguished from primary succession on new islands like Krakatau or Surtsey by the fact that the PML is embedded within a landscape full of terrestrial biota whereas islands are isolated terrestrial systems within an aquatic environment. From primary succession after volcanic activities it is divided by the fact that there is no solid rock which needs weathering before becoming a suitable substrate for vegetation. In principle, the sandy substrate of the PML is faster to be colonized by plants than solid rocks. The process of primary succession in the PML is therefore faster than in other sites with primary succession.

Facing these problems and views, SCHREIBER (1997) concludes that every process of succession is unique in space and time.

The relevance of soil as an important factor for the understanding of succession has already been stressed in former times (BRAUN-BLANQUET & JENNY 1926, KUBIENA

1948, KÜHNELT 1950). Soil ecologists were able to add new intelligence for the comprehension of succession (CURRY & COTTON 1983, TAMM 1986, KOBEL-LAMPARSKI 1987, GREENSLADE & MAJER 1993, MAJER & NICHOLS 1998, DUNGER 1998, TOPP 1998, DUNGER & WANNER 1999).

As ecosystems change from their native state to less natural ones, soil communities modify their quantitative and qualitative characteristics, and can signal the degree of alteration, degradation and substitution with respect to the original coenoses (MIGLIORINI et al. 2003).

If one's aim is to understand primary succession in soil, Collembola are the best objects of choice among microarthropods for researches, although some invertebrate zoologists are of the opinion that Collembola are rather dour unspectacular creatures (HOPKIN 1997):

- Collembola are extremely important in influencing the structure of some soils (RUSEK 1975).
- There already is a general understanding for succession of Collembola in other mining areas, mostly gained by the works of DUNGER.
- Due to their dispersive powers (HOPKIN 1997), Collembola are among the first colonisers in soil (e.g. DUNGER & WANNER 1999).
- High species diversity (about 420 species are known for Germany) is suitable at least for results on community level.

Collembola are considered to be suitable indicators for environmental change and for functional changes within soil communities (PFLUG & WOLTERS 2002). Yet it is generally agreed, that fauna communities rather than single species should be used to characterise sites (DUNGER 1968, 1989, EKSCHMITT 1998, PONGE 2003, FILSER 2003, pers. comm.). REBEK et al. (2002) even suggest a well-rounded approach to community study incorporating the life histories of many different soil organisms.

Distribution of Collembola is similar to other soil microarthropods. The fact must be kept in mind that soil is a three-dimensional environment. HOPKIN (1997) quotes USHER (1969) who showed, that only the least percentage of species (< 1 %), generally ubiquists, show a uniform distribution. Many species are distributed randomly, but the vast majority (>70 %) shows aggregated distribution. Aggregated distribution is probably mainly due to microclimatic conditions within a block of soil.

Despite the tendency to regard Collembola as rather sedentary creatures, they have an astonishing ability to disperse, especially by air (DUNGER 1989, HOPKIN 1997). The capability to immigrate by air makes Collembola successful early colonizers of reclaimed lands.

There are still many deficiencies concerning the knowledge about Collembola. It starts with the tendency to treat them as a new class "endognatha" instead of insects, undergoes constant systematical changes within the class (HOPKIN 1997, SHAW 1997) and ends up with lacking and contradictory autecological knowledge of many species (HOPKIN 1997, CASSAGNE et al. 2003). Fortunately, systematical changes do not affect the results of this study and there are only few species of minor importance for this study where there is still considerable lack of knowledge.

2. Research Programs

The data which were gained in this study are results of two research programs. Both research programs were mainly performed at the Brandenburg University of Technology, Cottbus.

2.1 Sonderforschungsbereich „Entwicklung und Bewertung gestörter Kulturlandschaften, Fallbeispiel Niederlausitzer Bergbaufolgelandschaft“ (SFB 565)

The SFB 565 (2001 – 2004) dealt with the question, if and how a sustainable development is possible in a cultural landscape after an extensive anthropogenic intrusion. 16 subprojects, dealing with social science and natural science, were established at the Brandenburg University of Technology, Cottbus, in an interdisciplinary approach to the problem. The PML of Lower Lusatia is the studied case.

Subproject B2 “Stochastische und deterministische Aspekte der faunistischen Besiedlung von Hochgrasbeständen und Sandtrockenrasen“ at the Chair of General Ecology dealt with diversity and peculiarity from an ecological point of view. The general aim of the study was a partitioning of stochastic and deterministic aspects of succession. The central question was: How long does it take to establish food chains in characteristic structures of the PML comparable to those in undisturbed sites? Exponents of different trophic levels are studied. The focus was on arthropoda and small mammals.

Research sites were sites with natural succession (dunes, psammophytic grassland, *Calamagrostis epigejos*-dominated grasslands), afforested sites (*Pinus sylvestris*) and reclaimed agricultural land.

2.2 Successional Change and Biodiversity Conservation in a Red Oak Chronosequence (SUBICON)

Succession and conservation of diversity in red oak forests (*Quercus rubra*) and reference sites in the PML are subjects of SUBICON (2001 – 2004). Genetic and biocoenotic diversity of different functional groups is studied within a chronosequence. Mechanisms for the maintenance and development of biodiversity are studied separately for different trophic levels of the ecosystem and finally correlated. Especially α-diversity of destruents, plants and chosen taxa of arthropods and small mammals is analysed and linked to β-diversity, intensity of disturbance, biotic interaction and genetic diversity.

Research sites were afforested (*Quercus rubra*) dumped sites in the PML of Lower Lusatia and reference sites on undisturbed land (*Quercus petraea, Q. rubra*).

At the end of the 19th century, the red oak (*Quercus rubra*) was imported from North America to Europe as a tree species with good growth even on poor soils. In the

process of recultivating the PML with woodland it played an important role: It was on 15 % of afforestation sites (PREUßNER 1998). In contrast to open habitats in the PML and despite their role in recultivation, red oak forests have not been studied systematically on their flora and fauna. SUBICON closes the gap in knowledge concerning the importance of red oak forests for biodiversity and the function of ecosystems in Europe. Red oak ecosystems are considered to be models for the development of biodiversity in forest ecosystems.

2.3 Aims and hypotheses

The major aim of this study is to document the succession of different ecological groups of Collembola and dominant species on acidic reclaimed land and to understand the general mechanisms and correlations which interact here. Moreover, general knowledge about the ecology of the species in question is to be gained. Two more questions have to be answered:

- When do communities on reclaimed land become similar to those of undisturbed sites?
- How do soil parameters change with time and how do they influence Collembola?

3. Materials and Methods

3.1 Study area

The post-mining area of Lower Lusatia is situated in the south-east of Brandenburg and north-east of Saxony, 130 km southeast of Berlin and 100 km north of Dresden (fig. 1). Predominant land use in the non-mining areas is forestry which covers about 70 % of the total area. In most parts of Lower Lusatia, agriculture is traditionally of minor importance as the soils are generally nutrient poor and infertile (MRZLJAK & WIEGLEB 2000). Climate is already influenced by the continent (GOLDLACK et al. 2000).

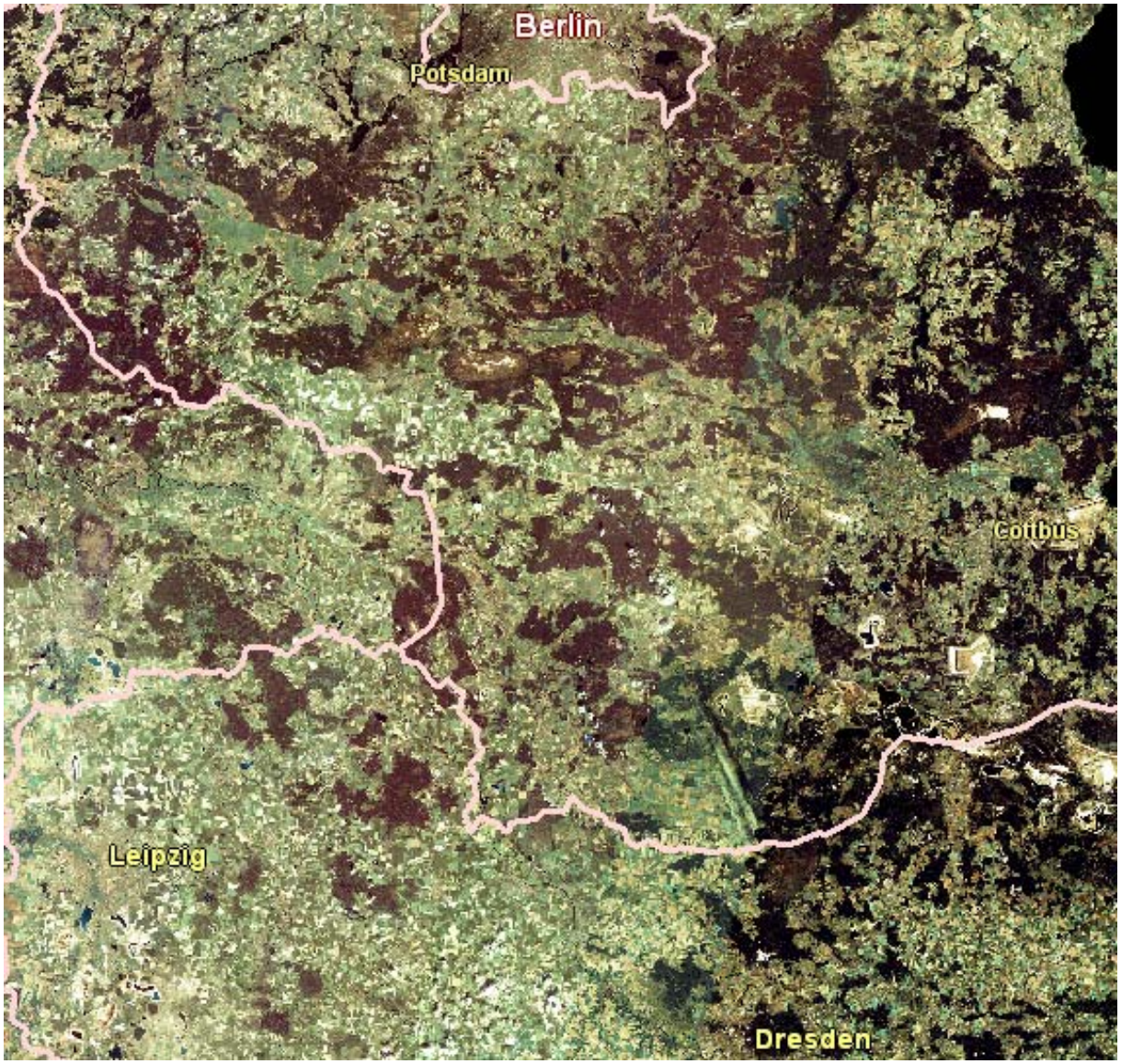


Figure 1: Study area Lower Lusatia (satellite image D-sat6, 2003).

Strip mining effectively disrupts decomposition and nutrient cycling processes by destroying the integrity of both soil and vegetation structure (PARSONS & PARKINSON 1986). Worldwide, reclamation studies on human-disturbed areas started in the second half of the 20th century, where the restoration of post-mining landscapes (PML) has been a challenge for scientists and engineers (WANNER & DUNGER 2002). The recultivation of post-mining landscapes, especially opencast coal mining areas, has been a severe problem and still is (e.g. DUNGER 1968, 1989, OLSCHOWY 1993, HÜTTL et al. 1996, PFLUG 1998, WIEGLEB & FELINKS 2000). Restoration of an ecosystem is a considerable intellectual challenge requiring that one understands not only the nature of the ecosystem itself, but also the nature of the damage and how to "repair" it (BRADSHAW 1999).

In the cultural landscape of Central Europe, former lignite mining areas are privileged sites with respect to the suitability for succession research. The mining impact is viewed as the heaviest one on land surface since the glacial epoch 10.000 years ago (WIEGLEB & BRÖRING 2001). Reclamation and renaturation of large devastated areas in the eastern parts of Germany are a striking example for the rearrangement of entire landscapes. The reorganization of dump substratum into a biologically active, sustainable soil is of foremost interest. Furthermore, the establishment of biotic communities within these newly developing areas is an interesting process of primary immigration and succession (DUNGER 1999).

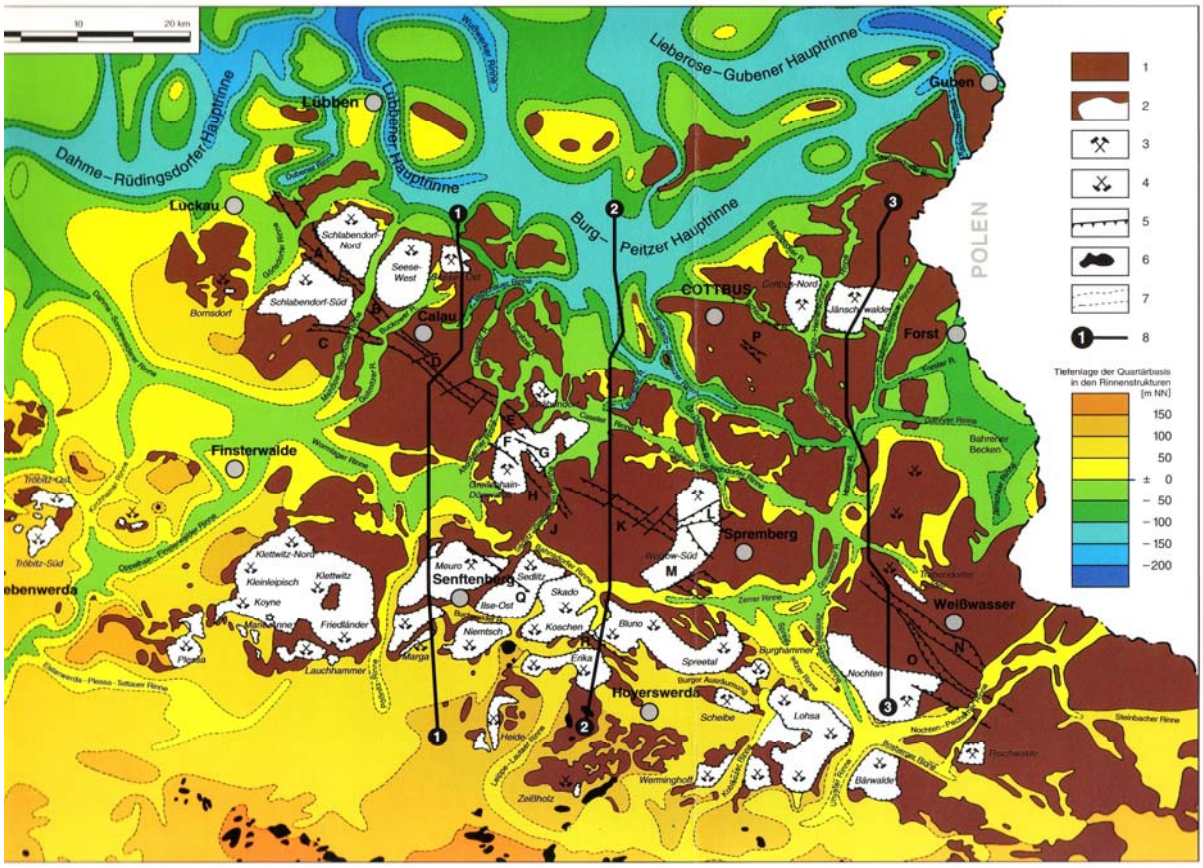


Figure 2: Lignite beds (brown) in Lower Lusatia (NOWEL et al. 1995).

The lignite dates back to tertiary (SCHRÖDER & NOWEL 1995). Lignite beds (Figure 2) are between 7 and 20 meters of thickness, with an average of 10 meters (NOWEL et

al. 1994). Mines were opened both in glacial valleys and moraine areas (MRZLJAK & WIEGLEB 2000). The thicknesses of the layers above vary from 35 meters in glacial valleys to 90 meters in moraine areas (GUNSCHERA et al. 1996). The area was strongly influenced by the Saalian and Weichselian glacial epochs (WIEGLEB & FELINKS 2001).

Lignite was first found near Lauchhammer in 1789, yet the industrial use of lignite began in the middle of the 19th century which caused a significant upturn in economy for the region. During the 40 years of the German Democratic Republic, lignite was the energy source of utmost importance. After German Reunification, 12 of 17 mines were closed down (FELINKS 2000).

The dumps consist mainly of tertiary and quaternary, sandy mineral substrates with a varying amount of coal (WIEGLEB & FELINKS 2001). Tertiary material of the second Miocene coal seam is sulphurous and acidic by pyrite oxidation which is not only a prominent problem for the Lower Lusatia region (SCHAAF et al 2000, KEPLIN & HÜTTL 2000) but also worldwide (e.g. MOORE & LUXTON 1988, PARSONS & PARKINSON 1986). In addition to low pH values, these sites are characterized by low levels of all nutrients (especially nitrogen, phosphorous, potassium and magnesium) and organic matter. The process of soil formation at most sites is at the very initial stages (WIEGLEB & FELINKS 2001). The substrates show a low maximum water retention capacity and high evaporation rates. Combined with high surface temperatures, this leads to very dry habitat conditions (KATZUR 1998). Because of the poor soil properties, ca. 60 % of the PML is dominated by afforestation (SCHAAF et al. 2000; *Pinus sylvestris* is the dominating tree in the afforested sites with 54 %, PREUßNER 1998).

The landscape is characterized by poor-quality *Pinus* forests (DUNGER 1989). To correct nutrient deficiencies and low pH, high amounts of lime and base rich lignite ash was incorporated into the substrates during melioration campaigns (up to > 1.000 dt CaO ha^{-1}; DREBENSTEDT, 1994; KATZUR & HAUBOLD-ROSAR, 1996).

Due to the conveyer belt technology, selective dumping of toxic and non-toxic material is not possible (HÄGE, 1996). This technology leads to a greater variety in soil properties in mined areas (KEPLIN & HÜTTL 2000) on a local scale (0 – 10m) than in unmined locations, with pH most variable. On a landscape level (500m) however, heterogeneity is smaller than in unmined areas (HARRANDINE 1949, SCHAFER 1979, WILDING & DREES 1983). Spatial variability of minesoil properties seems primarily random (WILDING & DREES 1983), but HOSSNER et al (1997) recognize it as systematic due to the mining technology, whereas heterogeneity of natural soils is caused by the interaction of different natural processes (ALLEN & HOEKSTRA 1991).

For many decades, ecosystems on lignite and pyrite containing substrates are dominated by substrate induced processes. Even after more than 50 years the sites show strong quantitative and qualitative differences compared to non-mine sites (SCHAAF et al. 1999).

3.2 Systematic of site-names

The name of each study site is tripartite, consisting of the first 3 letters of

1. the mining-area: Cot = Cottbus-Nord, Sch = Schlabendorfer Felder, Koy = Koyne, Ple = Plessa, Dom = Domsdorf;

2. structure/type of vegetation: **bar** = dune, bare substrate (vegetation cover < 10 %); **spa** = sparse vegetation, short grass, xeric grassland (vegetation cover 10 – 70 %); **den** = dense vegetation on meadow and waste land, *Calamagrostis epigejos*-dominated grassland (vegetation cover > 70 %); **pin** = afforestation with *Pinus sylvestris*, **oak** =afforestation with *Quercus rubra, Q. petraea*
3. and the age since last management: dumping/melioration/afforestation; refX = reference site X.

3.3 Mining areas

Five mining areas and woodland as reference site were used in this study (Figure 3). They are to the west of the city of Cottbus, only Cottbus-Nord is to the east.

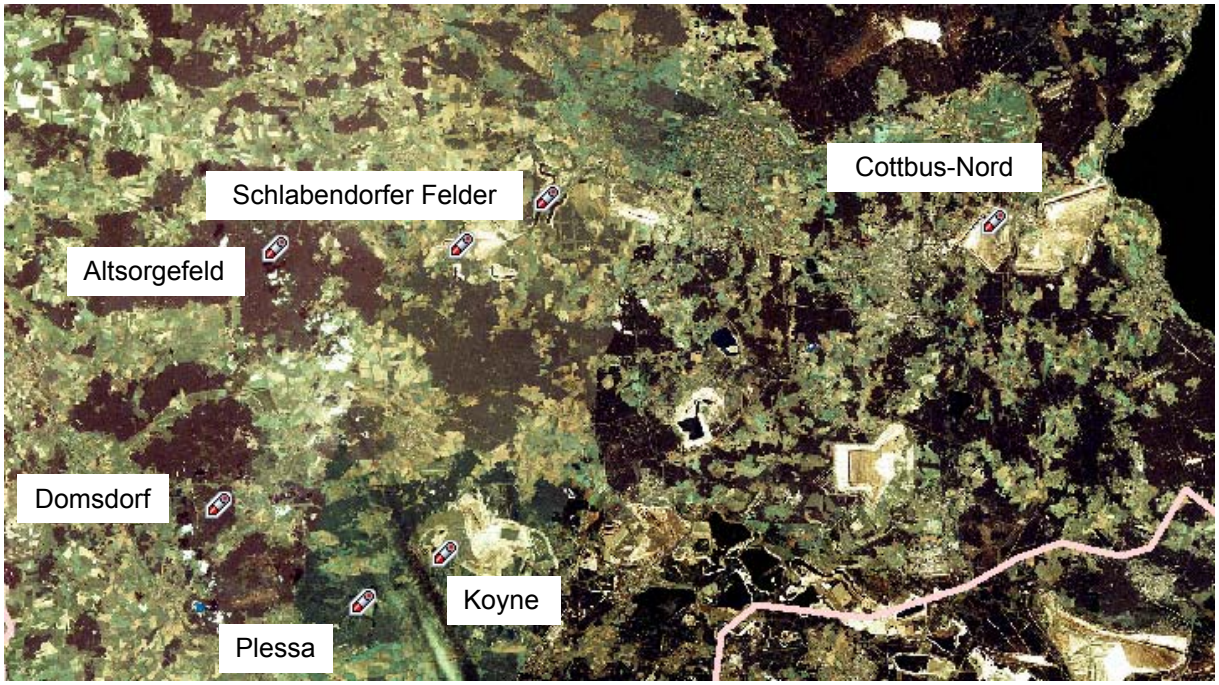


Figure 3: Studied areas (satellite image: D-Sat6, 2003).

3.3.1 Cottbus-Nord

The area (1.362 ha, E14° 26’ 46’’, N51° 46’ 58’’) is situated immediately to the north-east of Cottbus (Figure 4). The deep-well pumping began in 1975, first lignite was mined in 1981 (Braunkohlenausschuss 1994). After mining, the area will become mainly a lake. There are 2 study sites within the mining-area of Cottbus-Nord, which is the youngest one studied. The mining is still ongoing. To prevent neighbouring areas outside from dust emission, after general melioration seeds of grasses and herbs were sown into the bare substrate to enable the vegetation to cover the area faster. **Cot-den-13** is a dense *Calamagrostis epigejos*-dominated grassland (vegetation cover > 95 %). **Cot-spa-4** is almost bare sand, despite sowing still with sparse vegetation (vegetation cover ≈ 15 %).

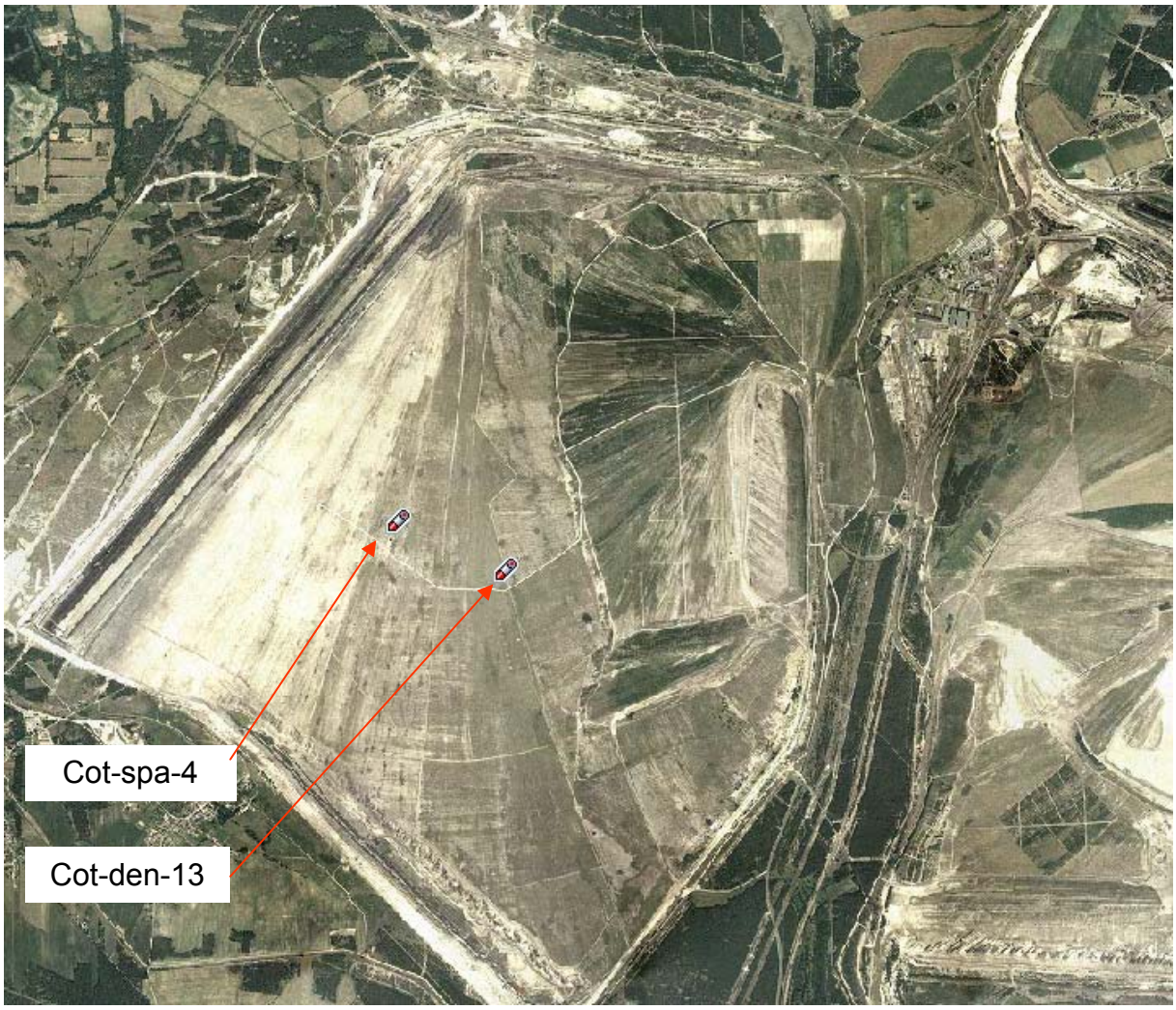


Figure 4: Mining-area of Cottbus-Nord and study sites. At the right margin the mining-area of Jänschwalde (satellite image: D-sat6, 2003).

3.3.2 Schlabendorfer Felder

The mining area of “Schlabendorfer Felder” is divided into a separate northern and southern area with the undisturbed area of the village Schlabendorf in the middle.

- Schlabendorf-Nord (E13° 51’ 50’’, N51° 48’ 57’’): In 1957, the deep-well pumping began and in 1961 the first lignite was mined. In 1977, the mine was closed down. Already in 1964 the reclamation was started. The rising of the ground-water level is supposed to be finished in 2020. In the east, the lake “Lichtenauer See” rises with the rising ground-water. Schlabendorf-Nord covers an area of about 25 km^2 (Abschlussbetriebsplan Schlabendorfer Felder, 1994). The reference site **sch-spa-ref** is moss-rich xeric grassland about 100 m to the east of the mining area. **Sch-den-8** is immediately at the bank of the rising lake, sub-samples A, C and E about 0 - 1 m from the water. As the water table rose, the sampling-site “moved” with the water table, so that A, C and E were always taken 0 – 1 m from the water. As an average, the water-table rose about 1 m per year. **Sch-pin-23** was dumped in 1975 and afforested in 1981 with *Pinus sylvestris*. **Sch-spa-29.1** is a xeric grassland rich with moss. This site is about 1 km from the next two sites. **Sch-spa-29** is

heterogeneous: 1/3 is almost bare of vegetation (sub-samples A + B) and 2/3 *Calamagrostis epigejos*-dominated grassland (sub-samples C – F). However, as *C. epigejos* invaded the site only recently, it was classified as "spa", because it was supposed that there was hardly any effect on the euedaphic community yet. **Sch-den-29** is *Calamagrostis epigejos*-dominated grassland with few pines. It is situated 100 m from **Sch-spa-29.1**. **Sch-den-23** is on waste land between a field with *Medicago sativa* and a hedgerow (sub-samples A, C, E about 1 m from the field, B, D, F about 1 m from the hedgerow). This area was meliorated with ashes in 1981. As the area was prepared for agriculture, melioration was performed with great care and precision. **Sch-oak-23** was afforested in 1981 with *Quercus rubra*. This afforestation was not successful in all parts. There are some clearings within the site with xeric grassland rich with moss. At this site, litter is accumulated from A – D to E and F, probably caused by a slight slope and the wind (Figure 5).

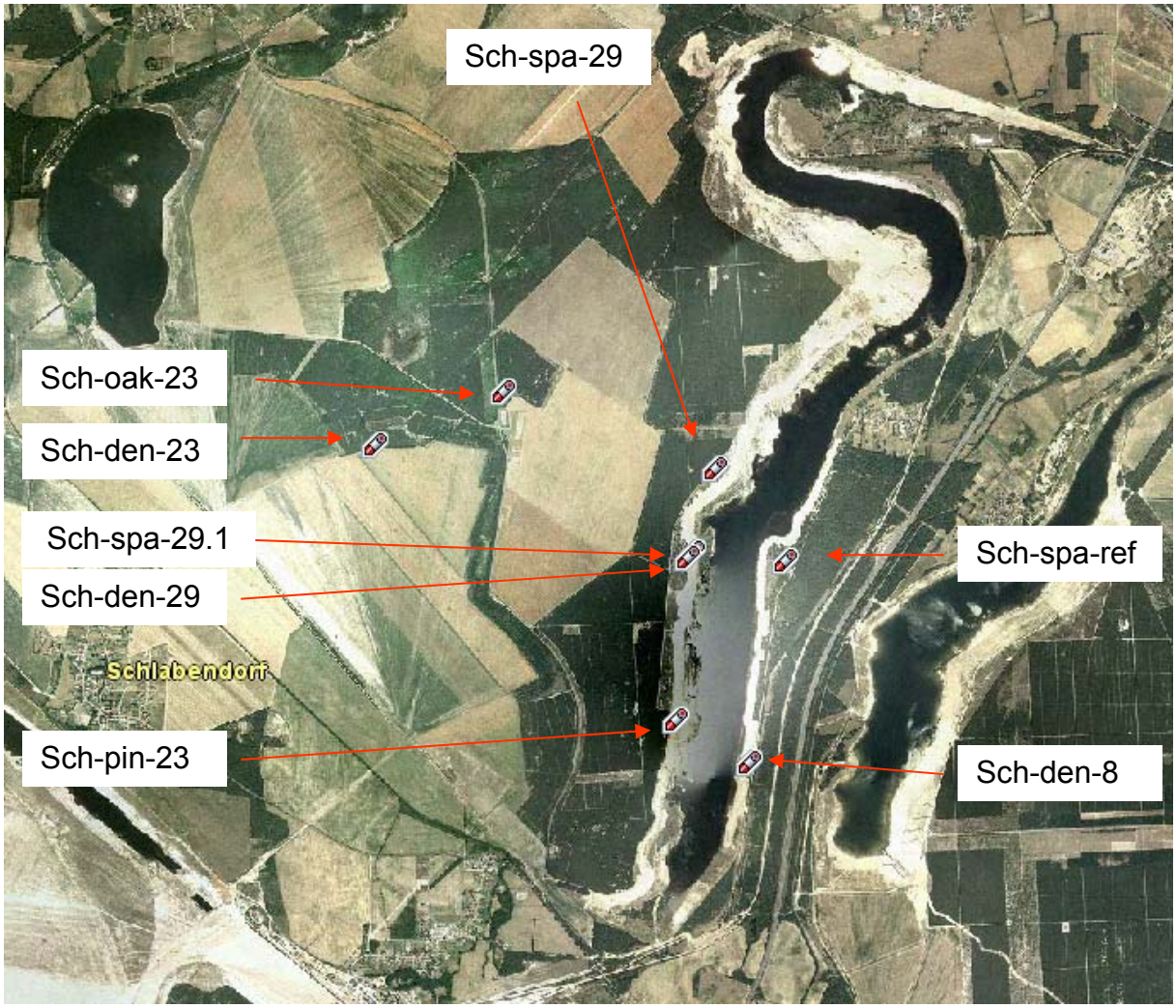


Figure 5: Mining-area of Schlabendorf-Nord and study sites. At the right margin the mining-area of Seese-West (satellite image: D-Sat6, 2003).

- Schlabendorf-Süd (E13° 45’ 33’’, N51° 46’ 11’’): Quaternary substrate from the southern part of the mining-area contains lime; therefore, pH is generally higher than in Schlabendorf-Nord. **Sch-den-ref1** is a dry meadow with one single cut per year. It is situated about 200 m to the south of the mining-area near Bergen. **Sch-den-ref2** is a *Calamagrostis epigejos*-dominated grasslands with few pines about 50 m south of the mining-area. It shows a gradient from sand to loam. Ten meters to the east there is a small depression which fills with water during winter. **Sch-spa-16** was dumped in 1985 and meliorated in 1988. It is a xeric grassland with sparse vegetation (vegetation cover ≈ 25 %). **Sch-den-16** is *Calamagrostis epigejos*-dominated grassland (vegetation cover ≈ 70 %).

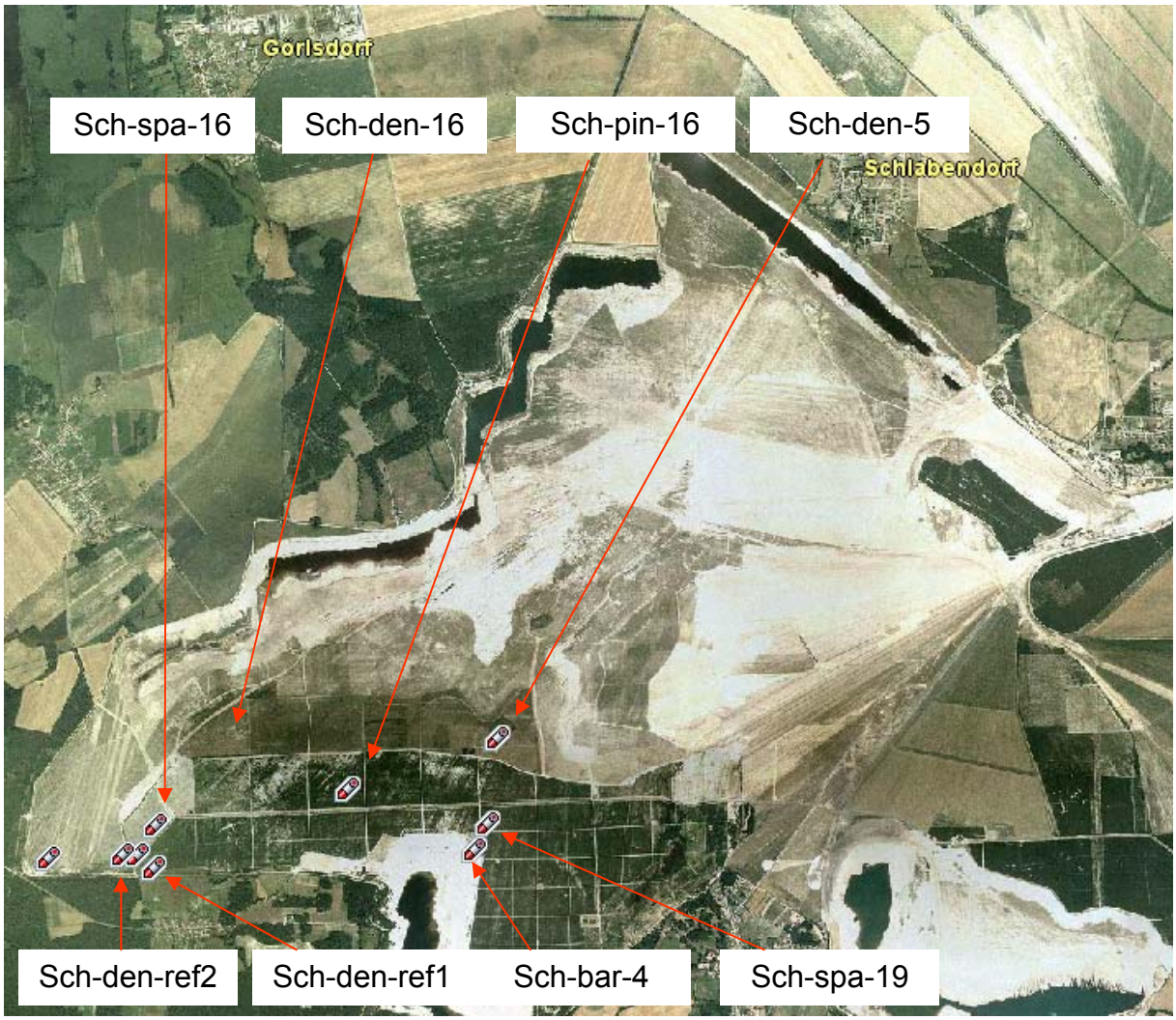


Figure 6: Mining- area of Schlabendorf-Süd and study sites (satellite image: D-Sat6, 2003).

It was also dumped in 1985 and meliorated in 1988. As it is situated at the bottom of a slope, the site’s microclimate is slightly moister than that of other sites. **Sch-pin-16** was treated as the former sites. It was afforested with pines in 1988. **Sch-bar-4** was dumped in 1985, but moved again in 2000. There was no apparent melioration and it is a dune of loose sand. **Sch-spa-19** was dumped in 1985, but not meliorated. It is a moss-rich xeric grassland with few

pines. **Sch-den-5** was dumped in 1985 and meliorated in 1999. Afterwards grasses and herbs were sown and it was afforested with *Quercus rubra* which did not grow well, most of the trees died off. This site will be used in both chronosequences, a) as youngest afforestation site and b) as a young site with dense vegetation (Figure 6).

3.3.3 Domsdorf

At the study site at Domsdorf (E13° 26' 57'', N51° 34' 25'') tertiary substrate was dumped in 1946. Soil conditions were poor with low pH and poor moistening of substrate, strong heterogeneity and few amounts of nutrients (FRIEDRICH-EBERT-STIFTUNG 1994). In 1961, the melioration was accomplished by the use of more than 1.000 t of lignite ash/ha/30 cm (GOLLDACK et al. 2000) and ca. 60 t of Ca/O/ha/20 cm (SCHAAF et al. 1999). Humus is mull-like moder (5 cm depth, pH 4.7; GOLLDACK et al. 2000). The site was afforested in 1967 with *Pinus* sylvestris. There is just one study site: **dom-pin-37** (Figure 7).

Figure 7: Mining-area of Domsdorf and study site (satellite image: D-Sat6, 2003).

3.3.4 Plessa

In the area of Plessa (E13° 38' 03'', N51° 29' 38''), lignite was mined from 1929 to 1958. The soil in Plessa contains lime and loam, so that the pH level is generally higher than in other sites. The sampling sites were dumped in 1945. **Ple-oak-43** was afforested in 1961 with *Quercus rubra*. The following 3 sites are on a steep dump ("Weißer Berg"), consisting of quaternary substrate: **Ple-bar-59** is a dune with bare sand which has not been colonized by plants since dumping. **Ple-pin-20** was a xeric grassland with surrounding pines when researches on this site began in 1995 within the LENAB-project. Meanwhile the pines grew up, so that the site has the character of a young (approximately 20 years) pine forest. In this study, it will be considered as pine woodland. **Ple-den-59** is a *Calamagrostis epigejos*-dominated grassland with pines. Similar to the former site, it might be looked upon as clearing in a young pine forest. The 3 sites on this dump are about 100 m away from each other in a straight line (Figure 8).

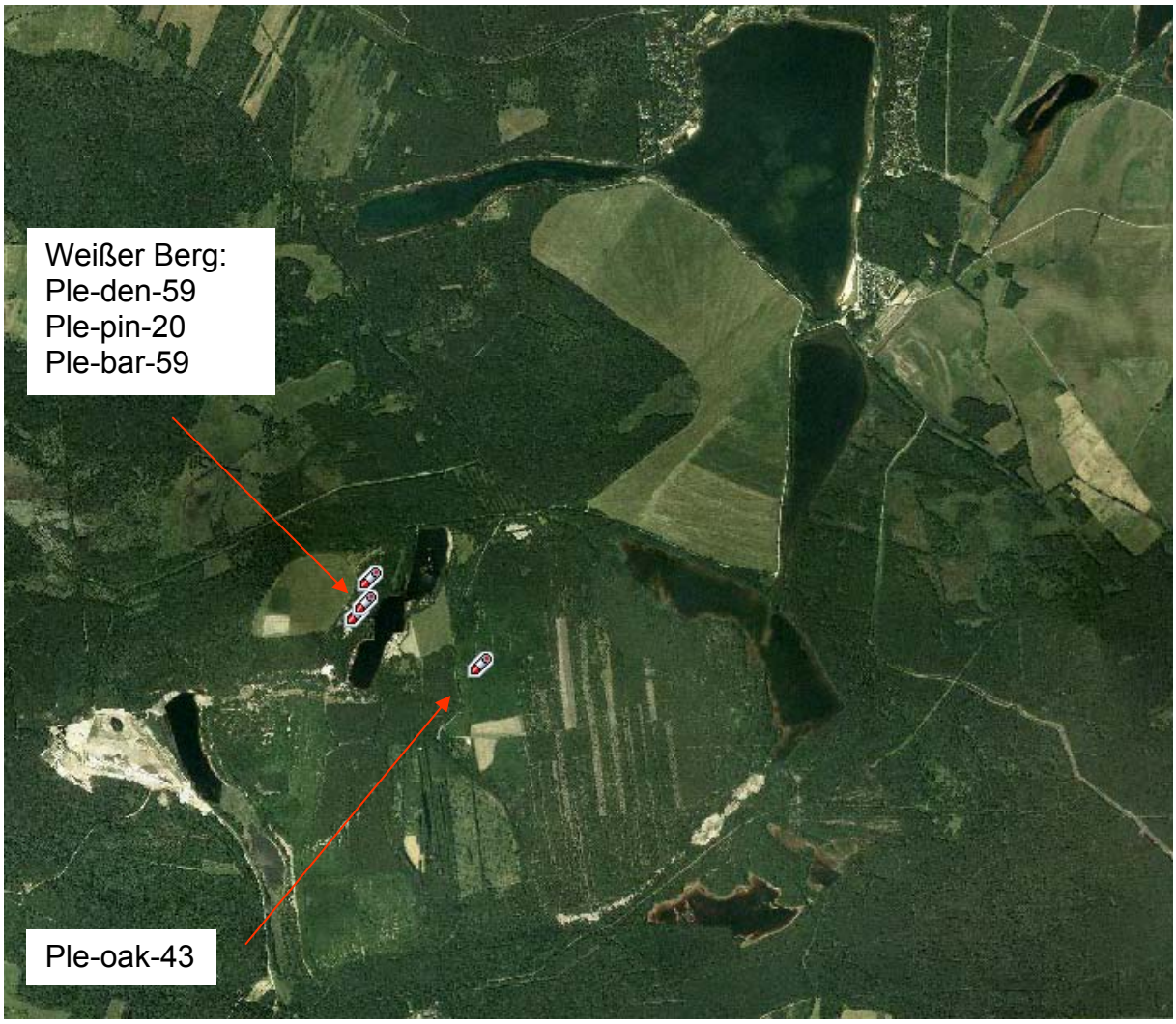


Figure 8: Mining-area of Plessa and study sites (satellite image: D-Sat6, 2003)

3.3.5 Koyne

The mining-area of Koyne (E13° 44' 26'', N51° 31' 52'') is situated to the north of Lauchhammer. It is divided into a vast number of small sub-mining areas. The mine "Koyne" was run from 1921 to 1958. The soil was dumped in 1950. **Koy-bar-54** is an area with sparse vegetation (cover < 10 %). Erosion formed deep troughs, so that the structure of this site is most heterogeneous. **Koy-oak-24** was afforested in 1980 with *Quercus rubra*. In 1970, **Koy-oak-34** was also afforested with *Quercus rubra*, but before the soil had been meliorated with ashes. In October 2002, a large part of the oak-stand was stubbed and as a result, the sampling site was no longer within the oak stand but at its immediate border. Therefore, the sampling site was moved deeper into the wood again for constancy of environmental conditions.

The second investigated sub-mine was Tagebau IV which was run from 1921 to 1944. **Koy-den-54** is dense *Calamagrostis epigejos*-dominated grassland. It is a large clearing within woodland of birch and pine. The soil has a well developed root penetration. It is the only site in the PML where pseudo-scorpions were found (Figure 9).

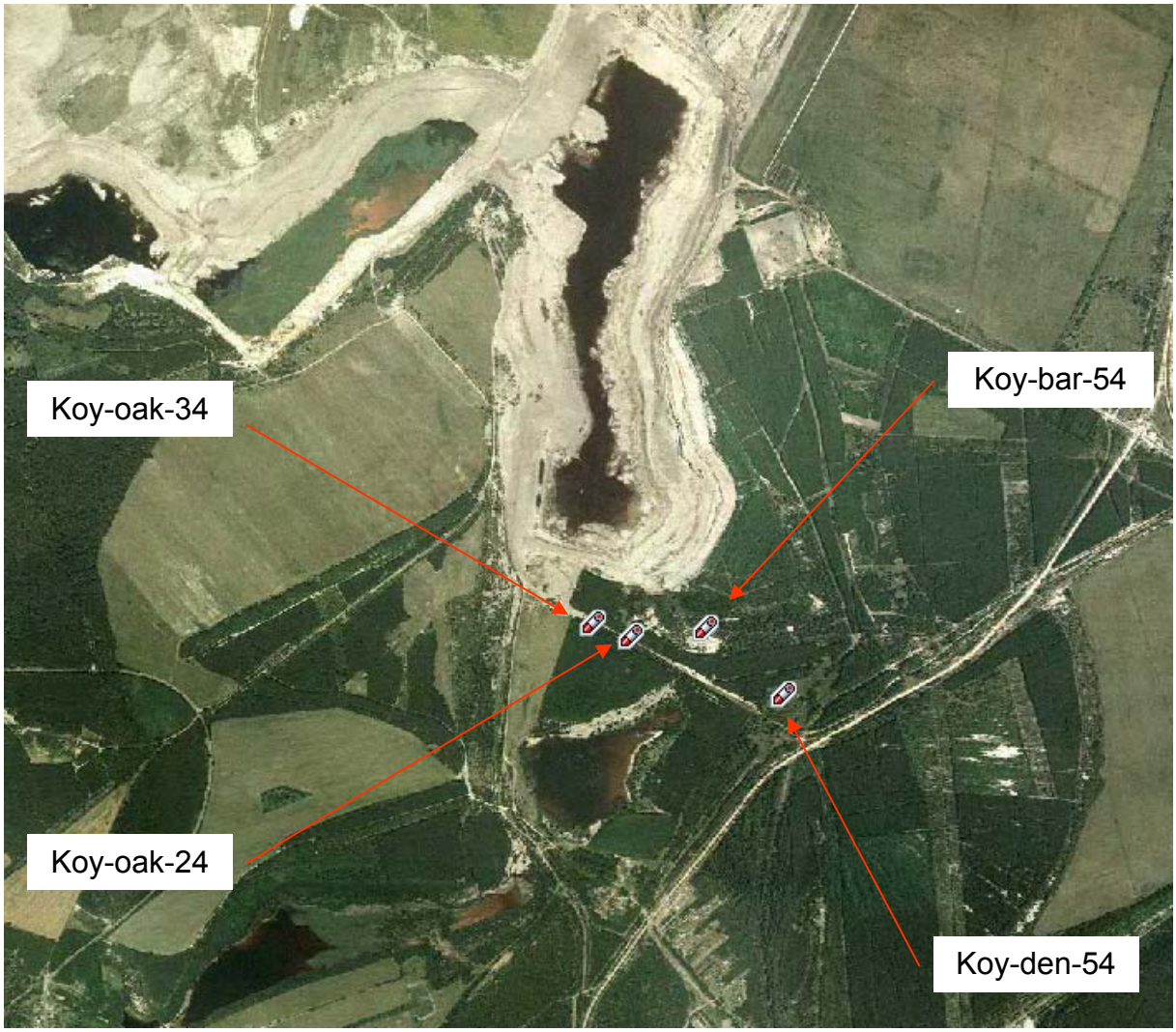


Figure 9: Part of the vast mining-area of Koyne and study sites (satellite image: D-Sat6, 2003).

3.4 Reference site Altsorgefeld

The large woodland of Altsorgefeld (E13° 31' 56'', N51° 46' 23'') is on undisturbed land about 23 km to the west of the next mining area (Schlabendorfer Felder). It is used as reference site for the afforestation chronosequence. The soil is sand and therefore the texture is comparable to the mining areas. However, pH of none of the meliorated areas is as low as that in Altsorgefeld. **Alt-oak-29** is a young oak afforestation with *Quercus petraea* and *Vaccinium myrtillus*, afforested in 1975. **Alt-oak-44** was afforested in 1960 with *Quercus rubra* and **alt-oak-00** is a *Quercus petraea* stand of at least 100 years of age. The three sites are relatively close to each other, **alt-oak-44** to **alt-oak-00** about 150 m and **alt-oak-00** to **alt-oak-29** about 300 m (Figure 10).

Figure 10: The vast woodland of Altsorgefeld and study sites (satellite image: D-sat6, 2003).

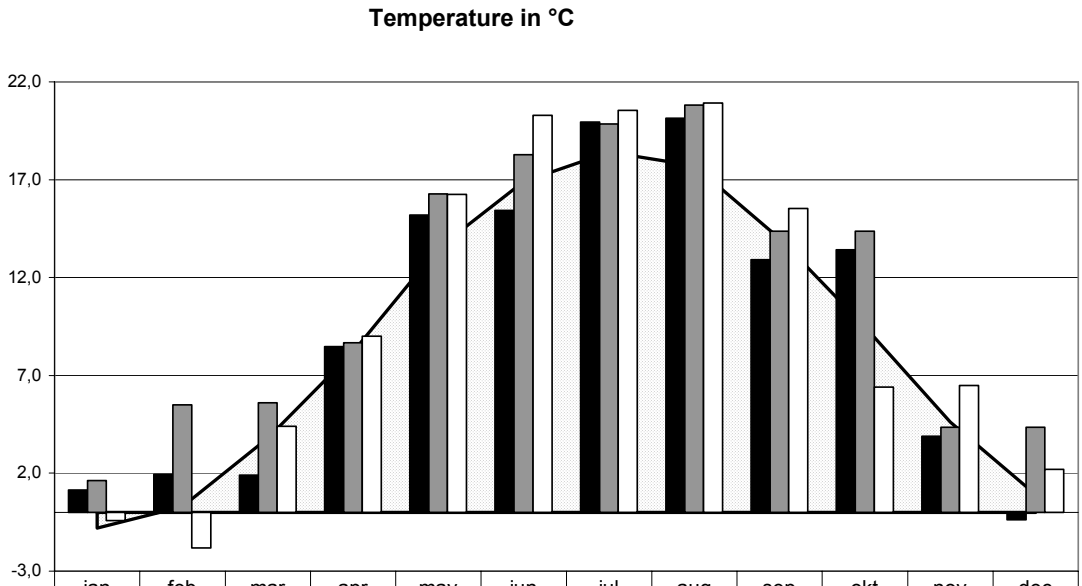
3.5 Climate

Climate, especially precipitation and its effect on soil moisture is critical for soil communities in sandy soils (HAGVAR & ABRAHAMSEN 1984, PARSONS & PARKINSON 1986, JUCEVICA & MELECIS 2002, PETERSEN et al. 2004). Therefore, data about temperature and precipitation were collected. For the year 2001, the data are from a meteorological station in Cottbus (DEUTSCHER WETTERDIENST). Since 2002, data have been available from a meteorological station in Zinnitz (BTU Cottbus) which is situated between the mining areas of Schlabendorf-Nord, Schlabendorf-Süd and Seese-West. As this station was much closer to most study sites, data from this station were taken for 2002 and 2003. Results of influence of climate and Collembola will be published in a separate work.

3.5.1 Temperature

From 1961 to 1990, the mean temperature per year in Cottbus was 8.9 °C. During the researches from 2001 to 2003, the mean temperature was 9.5 °C (Cottbus), 11.2 °C and 10.0 °C respectively (weather station Zinnitz). Figure 11 shows the mean temperature per month.

During the research period, all years were warmer than the average (mean from 1961 – 1990), especially 2003 (Figure 11).

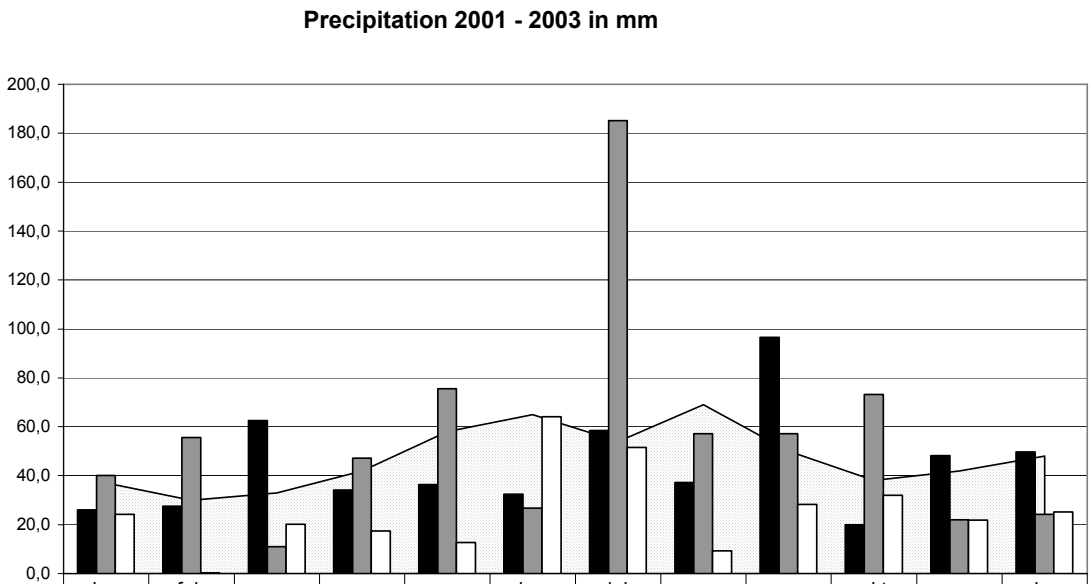


	jan	feb	mar	apr	may	jun	jul	aug	sep	okt	nov	dec
mean 1961-1990	-0,8	0,3	3,8	8,2	13,5	16,9	18,4	17,7	14,0	9,5	4,6	0,9
2001	1,1	1,9	1,9	8,5	15,2	15,4	19,9	20,1	12,9	13,4	3,9	-0,4
2002	1,6	5,5	5,6	8,7	16,3	18,3	19,9	20,8	14,4	14,4	4,3	4,3
2003	-0,4	-1,8	4,4	9,0	16,3	20,3	20,6	20,9	15,5	6,4	6,5	2,2

Figure 11: Mean temperature per month in Cottbus from 1961 to 1990 (area diagram), 2001 to 2003 in columns (data taken from DEUTSCHER WETTERDIENST and BTU Cottbus).

3.5.2 Precipitation

Mean precipitation per year from 1961 to 1990 in Cottbus was 566 mm. During the research period from 2001 to 2003, precipitation was 529 mm (Cottbus), 675 mm and 307 mm respectively (weather station Zinnitz). Thus, only 2001 can be regarded as an average year (93.5 %), whereas 2002 was too wet (119.2 %) and 2003 much to dry (54.2 %). The higher amount of precipitation in 2002 was mainly caused by a single thunderstorm on July 12th, which caused much havoc in the area Berlin/Brandenburg. Without this single event, 2002 would also have been an average year. In 2003, all months were much too dry with the exceptions of June (98.6 %) and July (95.6 %). February was the driest month with hardly any precipitation at all (0.7 %; Figure 12).



	jan	feb	mar	apr	may	jun	jul	aug	sep	okt	nov	dec
mean 1961-1990	37,0	30,0	33,0	42,0	58,0	65,0	54,0	69,0	50,0	38,0	42,0	48,0
2001	26,1	27,5	62,5	34,1	36,3	32,5	58,5	37,2	96,5	20,0	48,2	49,7
2002	40,0	55,7	11,0	47,2	75,5	26,7	185,2	57,1	57,2	73,2	22,0	24,1
2003	24,1	0,2	20,1	17,4	12,6	64,1	51,6	9,3	28,3	31,9	21,8	25,2

Figure 12: Mean precipitation per month in Cottbus from 1961 to 1990 (area diagram), 2001 to 2003 in columns (data taken from DEUTSCHER WETTERDIENST and BTU Cottbus).

3.6 Chronosequences

Chronosequences or false-time-series are often used where long time researches are not possible, generally for lack of time and/or money (e.g. SCHAAF et al. 1999, MRZLJAK & WIEGLEB 2000, PFLUG & WOLTERS 2002, FISCHER et al. 2002, JUCEVICA & MELECIS 2002, TROFYMOW et al. 2003). Ideally, a successional study should be based on a single site studied over an extended period of years in such a manner that faunal and floral communities could be monitored independently, but in relation to a known successional time scale (PARR 1978).

Two chronosequences were established:

a) **12 afforested sites**: 9 afforested sites in 4 different mining areas (see chapter 3.3) were chosen for the chronosequence, 5 had been afforested with *Quercus rubra* and 4 with *Pinus sylvestris*. The sites were afforested between 1961 and 2000. Stand age equals ± site age and therefore soil age. The only exception is **ple-pin-20**, where stand age is approximately 20 years, but site age > 50 years. Within this chronosequence, structure of sites follows age of sites.

   Another 3 afforestation sites were chosen as reference sites in the undisturbed woodland of Altsorgefeld. There, an old *Quercus petraea* stand (> 100 years), a *Q. rubra* stand afforested in 1960 and a *Q. petraea* stand afforested in 1975 were chosen. Within the chronosequence of 12 sites, the reference sites count as “oldest” sites.

   According to stand age, **alt-oak-29** is obviously younger than some sites in the PML. However, the forest soil of **alt-oak-29** is considerably older than that of all mining sites. Therefore, the reference sites are considered as oldest sites.

b) **19 sites of free succession**: These sites were chosen from 5 mining areas (see chapter 3.3). The sites were dumped between 1945 and 2000. As structure does not follow age of sites, a structural chronosequence was established. Study sites were distinguished after their structure in sites bare of vegetation (cover < 10 %), sites with sparse vegetation (cover > 10 % to 70 %) and sites with dense vegetation (> 70 %). The gradient from bare substrate to dense vegetation represents the classical model of vegetational succession. Although this model is criticised by some authors (PARR 1979, FELINKS 2000), the linear model seems best for a first approach to understand Collembolan succession. As the 3 structural types were arranged by age, there are 3 sub-chronosequences, one for each vegetation structure. 3 reference sites were chosen on undisturbed land near the border of the mining area of Schlabendorfer-Felder and regarded as “oldest” one within each sub-chronosequence. As there was no natural dune near the PML to be found, there is no reference site to the structure type “bare”. In addition to the reference site with dense vegetation, a second reference site was chosen in a dry meadow. Thus, there are 2 reference sites for the structure type “dense”, both close to each other.

Although sampling took place from 2001 to 2003, the sites remained approximately unchanged except for **cot-spa-4** which developed from bare sand to a side with sparse vegetation due to the sowing of herbs and grasses. It can be regarded as link between sites bare of vegetation and sites with sparse vegetation in structure and the youngest site with sparse vegetation.

3.7 Sampling

3.7.1 Sampling design

As one main aim of the projects SFB 565 and SUBICON was to correlate different trophic levels, the sampling design had to be a compromise for all researches. The study sites and sampling design had to be suitable for botany, zoology and soil ecology. Certain types of biotopes and age had to be included in the design. In the

end, the sampling design resembled a compromise which was agreeable for researches on small mammals, different arthropods and soil mesofauna, although much more comparable soil conditions would have been preferable.

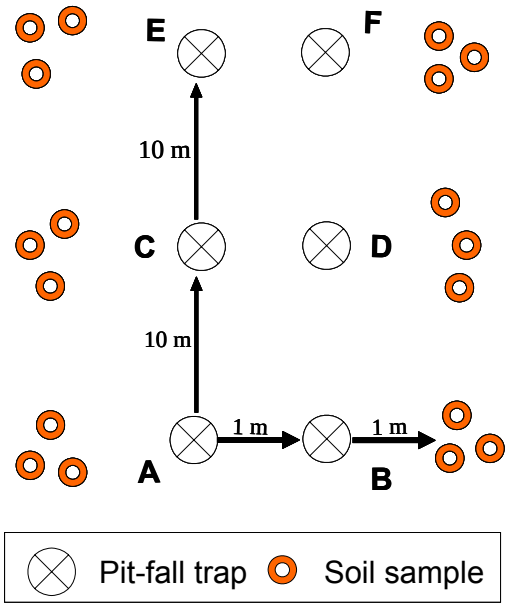


Figure 13: Sampling design.

In 30 sampling sites, 3 pairs of pit-fall traps were arranged in a regular pattern (each pair of 1 m distance being 10 m away from each other) within homogenous vegetation structure (MRZLJAK & WIEGLEB 2000). Soil samples were taken about 1 m to the left and right of each pair. In the end, soil samples were taken as 3 pairs, each pair of 3 m distance being 10 m away from each other.

3.7.2 Extraction of Collembola

Samples were taken from April to November. In this it was hoped to include species with different life cycle patterns and to get a representative picture of the species composition. From each study site, 24 to 36 soil cores were taken. For practical reasons (limited technical equipment) the number of samples could not be increased.

To reduce the compression of the sample when the soil corer (7.8 cm in diameter, ≈ 48 cm^2) was inserted into the soil, the lower part of the corer was slightly conical, allowing the sample to move with only small resistance within the cylinder. First, a soil corer of stainless steel was obtained from a current dealer. As already the author's own experiences at the Hochschule Vechta proofed, stainless steel is not rugged enough to withstand the mechanical needs. Therefore, a new corer of high-grate steel was made in the university's locksmithery (Figure 14). The soil core was pushed out gently with a piston and immediately divided into 2 layers of 5 cm each. These were transported and stored in PVC rings, with both ends tightly covered by metal lids.

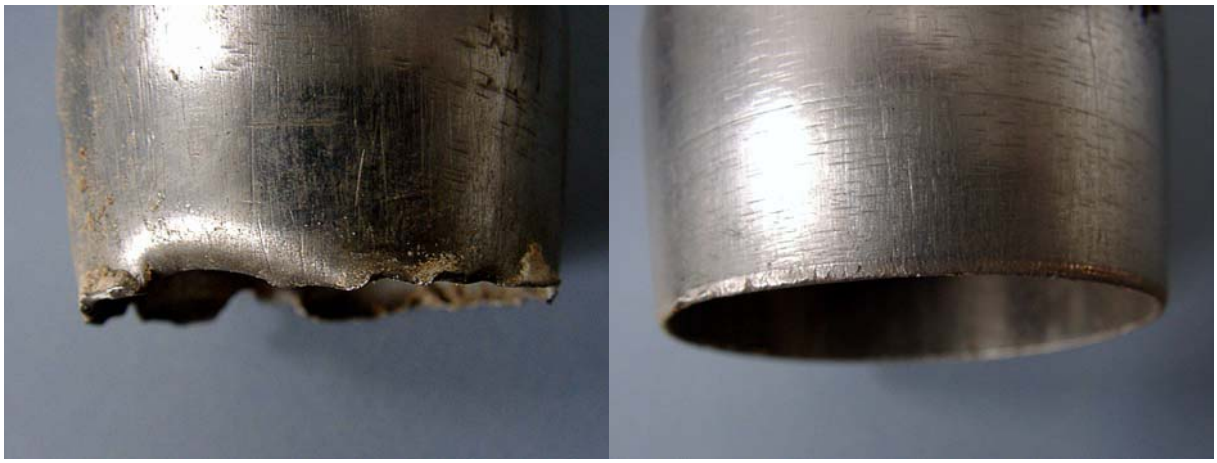


Figure 14: Soil corer of stainless steel (left), high grate steel (right).

The samples were stored for no longer than 24 hours at 8°C. Extraction was performed in a high gradient devise according to MACFAYDEN (1961) which was slightly adapted (FIRMA ECOTECH, Bonn). The sample was cooled by moist air from a fridge (≈ 12°C) and heated from above by dry air. The extraction lasted one week, with the temperature gently rising from 20°C - 25°C (depending on room-temperature) to 40°C after 7 days (Parsons & Parkinson 1986), with a gradient of at least 10°C from top to bottom of the samples. The animals were caught in 80 % ethanol for conservation. The jar with ethanol was removed after the 7 days.

The extracted Collembola were taken out of the ethanol using a small brush and for further determination again stored in 80 % ethanol. For determination the Collembola were sent to H.-J. SCHULZ (Naturkundemuseum Görlitz, Germany) and M. STERZYNSKA (Museum and Institute of Zoology, Polish Academy of Sciences, Warszawa, Poland).

3.7.3 Statistics

Dominance

Within each biocoenosis, individuals of different species are differently common. The relative abundance within the community is its dominance; the order from the most abundant to the rarest species is the scale of dominance of the biocoenosis (MÜHLENBERG 1989). A scale of dominance according to ENGELMANN (1978) was used in this work. He proposed the general usage of a variable, logarithmic scale. Its basis is a logarithmic function. The equidistant intervals of the logarithmic scale are chosen so that the dominant steps always comprise 85 % of the examined specimens. The results of researches are therefore more comparable by means of quantification (ENGELMANN 1978). The dominance classes used are:

- eudominant 40,0 – 100,0 %
- dominant 12,5 – 39,9 %
- subdominant 4,0 – 12,4 %
- recedent 1,3 – 3,9 %
- subrecedent < 1,3 %

Cluster analysis

Cluster analysis is an analytic procedure whose main purpose is to develop meaningful aggregations, or groups, of entities based on a large number of interdependent variables. The procedure creates groups using one of many different clustering strategies that maximises within-group similarity and minimises between-group similarity (MCGARIGAL et al. 2000).

Cluster analysis (software SYSTAT 9) of non-transformed abundance data (Ward's methods, chi-square distance) was performed to compare the data (PONGE et al. 2003).

Correlation analysis

For statistics, the software SPSS 12.0 was used. When it can be assumed that 2 variables are not normally distributed, the Spearman-Rho correlation is used. If there is no association between the 2 variables, r = 0, absolute correlation leads to r = 1. The correlation r coefficient is a number between +1 and -1. This number tells us about magnitude and direction of the association between 2 variables, the closer to +1 or -1, the higher the correlation. If the correlation is 0 or near 0, there is no correlation between the 2 variables. The direction shows if the correlation between the variables is positive or negative. P shows significances.

SPSS shows a significance, if $p < 0.050$. But also strong correlations, which are not necessarily significant in strict sense, can be helpful to explain observations. Therefore, also moderate correlations or "tendencies" ($p < 0.080$ to $p > 0.050$) were registered.

A vast number of parameters were tested for correlations: Soil parameters, ecological groups, life forms and dominances of each species were tested against each other.

3.7.4 Ecological groups of Collembola

For research on community level, 5 ecological groups of Collembola were distinguished:

1. species typical for forests
2. species typical for open habitats
3. hygrophilous species
4. eurotopic species
5. other species (juveniles, species without sufficient autecological data)

Similar groups were distinguished by RUSEK (1989), STERZYNSKA & KUZNETSOVA (1997) and CHERNOVA & KUZNETSOVA (2000). STERZYNSKA & KUZNETSOVA (1997) call these groups "ecofunctional groups" and distinguish further ruderal, compost, corticolous and myrmecophilous species.

Although there are species, which can be considered typical for disturbed sites (CHERNOVA & KUZNETSOVA 2000), most of these species are found in decaying organic matter and are presumably no good indicators for the disturbance of the mine

soils studied in this work. Therefore, this classification was not used and species as *Proisotoma minuta* were classified accordingly to the 5 classifications above.

Moreover, it was tried to distinguish 2 main life forms of Collembola:

1. epigaeic
2. endogaeic

Dominances and abundances will be calculated separately for the 2 life forms in order to show the dominating species in both groups. The life form hemiedaphic was not used, as vertical distribution of many species is due to environmental factors and time (HOPKINS 1997).

The categories for ecological groups and life forms are based on literature, mainly the works of DUNGER (1991, 1998, 2001), FJELLBERG (1980, 1998), PONGE (1991, 1993, 1998) and RUSEK (1992, 1995, 2004). For details, see the table in chapter 9.

3.8 Soil properties

For soil chemistry, many physico-chemical parameters can be measured. For soil biology and especially for Collembola researches, two parameters have proven to be of most importance: pH-value and organic matter content (HAGVAR 1982, HUTHA et al. 1983, HAGVAR & ABRAHAMSEN 1984, PARSONS & PARKINSON 1986, HAGVAR 1995, STERZYNSKA & EHRNSBERGER 2000, DUNGER et al. 2002, SHAW 2003). Considering the history of the study sites, both parameters seem best fitting to give a brief characterisation of the post-mining areas. ZERLING (1990) used the proportion of skeletal grains to proof comparability of his study sites. But EKSCHMIDT et al. (2003) showed that the proportion of skeletal grain is no good parameter for researches on Collembola. So a proportion of skeletal grain was not used in this work.

In addition to the standard parameters, water content, water capacity, electric conductivity, nitrate and phosphate were measured. Structure is defined as age of soils after dumping/last management (see arrangement of the chronosequence, chapter 3.6) whereas stand age is defined as the age of the woods. All parameters were tested for correlations (Spearman-Rho).

For the study of soil properties, soil was taken to a depth of 10 cm at the usual sampling sites, air-dried, and sieved. Generally, 6 to 10 samples were taken, depending on the team member who took the samples. Each sample was measured twice.

The material ≤ 2.0 mm was homogenized for further analyses (PONGE et al. 1993). pH_{CaCl} was measured with an electronic device. For organic matter content the samples were weighed and incinerated at 800°C for 3 hours. Organic matter was calculated from mass loss after ignition (SHAW 1997).

4. Results

4.1 Soil parameters

4.1.1 Chronosequence 1: Afforested sites

4.1.1.1 pH

In general, pH differs between 2.7 in Altsorgefeld and 6.7 in Plessa (tab. 1). It decreases significantly with time ($r = -0.7$, $p < 0{,}014$) and is negatively correlated to most other properties but phosphate which is positively correlated ($r = 0.7$, $p < 0.007$) (tab. 9). Soils which are most acidic are those from the old deciduous forest (e.g. PONGE et al. 2003) whereas the young reclamation sites were meliorated with lime (for the arrangement of the chronosequences, see chapter 3.6).

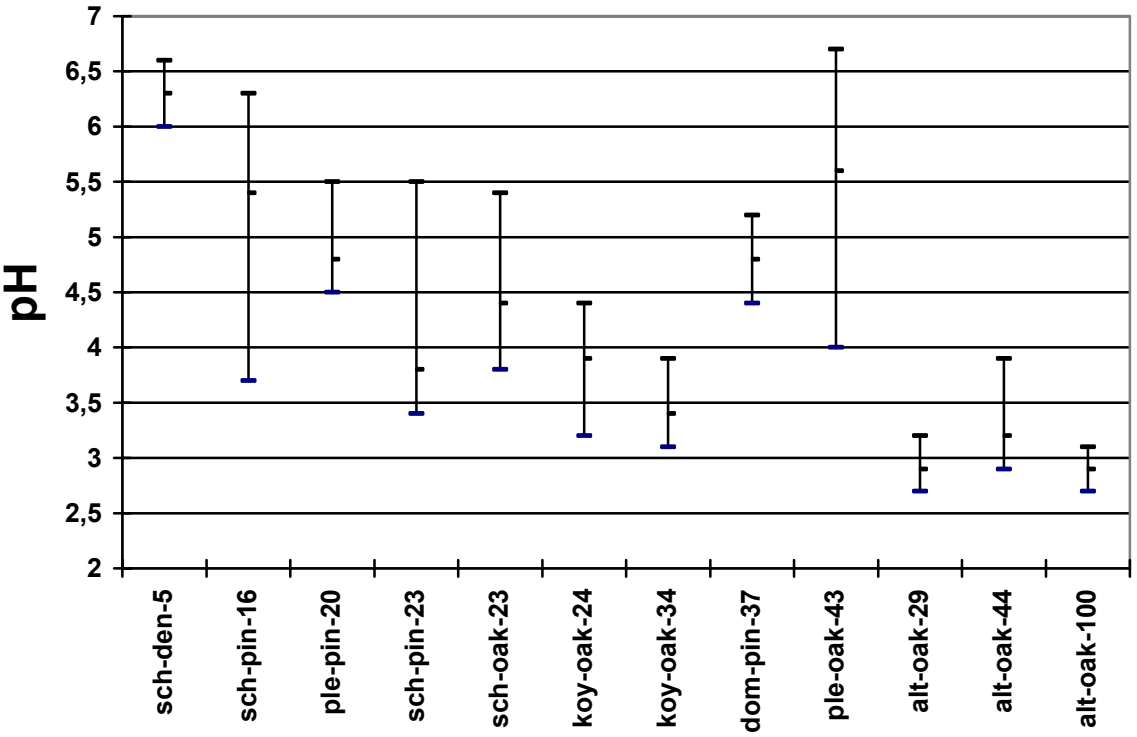


Figure 15: pH of afforested sites, youngest sites from left to right and reference sites to the very right of the x-axis, minimum, mean and maximum values.

In the process of weathering and leaching, pH generally decreases after melioration. Sites with strong buffering properties as ash meliorated ones tend to be more resistant towards weathering (**dom-pin-37**). Sites with quaternary substrate containing lime and therefore high original pH are also less affected by pyrite weathering (**ple-oak-43**). Still, the reference sites at Altsorgefeld with their old humus layers on sand, which has a poor buffering capacity, have the lowest pH in the chronosequence (Figure 15: pH of afforested sites, youngest sites from left to right and reference sites to the very right of the x-axis, minimum, mean and maximum values.).

Table 1: pH of the afforested sites, minimal, maximal and mean values, deviation and number of tested samples (n).

pH	min.	max.	mean	deviation	n
sch-den-5	6,0	6,6	6,3	0,15	12,00
sch-pin-16	3,7	6,3	5,4	0,96	12,00
ple-pin-20	4,5	5,5	4,8	0,31	12,00
sch-pin-23	3,4	5,5	3,8	0,78	12,00
sch-oak-23	3,8	5,4	4,4	0,50	12,00
koy-oak-24	3,2	4,4	3,9	0,41	12,00
koy-oak-34	3,1	3,9	3,4	0,27	12,00
dom-pin-37	4,4	5,2	4,8	0,29	12,00
ple-oak-43	4,0	6,7	5,6	0,92	12,00
alt-oak-29	2,7	3,2	2,9	0,14	22,00
alt-oak-44	2,9	3,9	3,2	0,23	36,00
alt-oak-100	2,7	3,1	2,9	0,11	21,00

Deviation is least in the undisturbed soils in Altsorgefeld, the youngest site and the ash-meliorated soils in **koy-oak-34** and Domsdorf. Highest variance is found in soils where quaternary material with originally high pH was mixed with pyrite-containing substrate and meliorated sites where weathering has already begun (**sch-pin-16**, **ple-oak-43**, **Fehler! Verweisquelle konnte nicht gefunden werden.**).

4.1.1.2 Organic matter content

Organic matter content calculated as loss on ignition increases significantly with stand age ($r = 0.9$, $p < 0.000$). It is also strongly correlated to all other properties but phosphate (very weak negative correlation) and pH (negatively correlated; tab. 9). But even after 43 years of afforestation on reclaimed land, organic matter content is lower than the one from the 29 year old stand on reference site in Altsorgefeld. Only **dom-pin-37** with its ash-meliorated soil shows a similar loss an ignition as the undisturbed sites on sand (fig. 16).

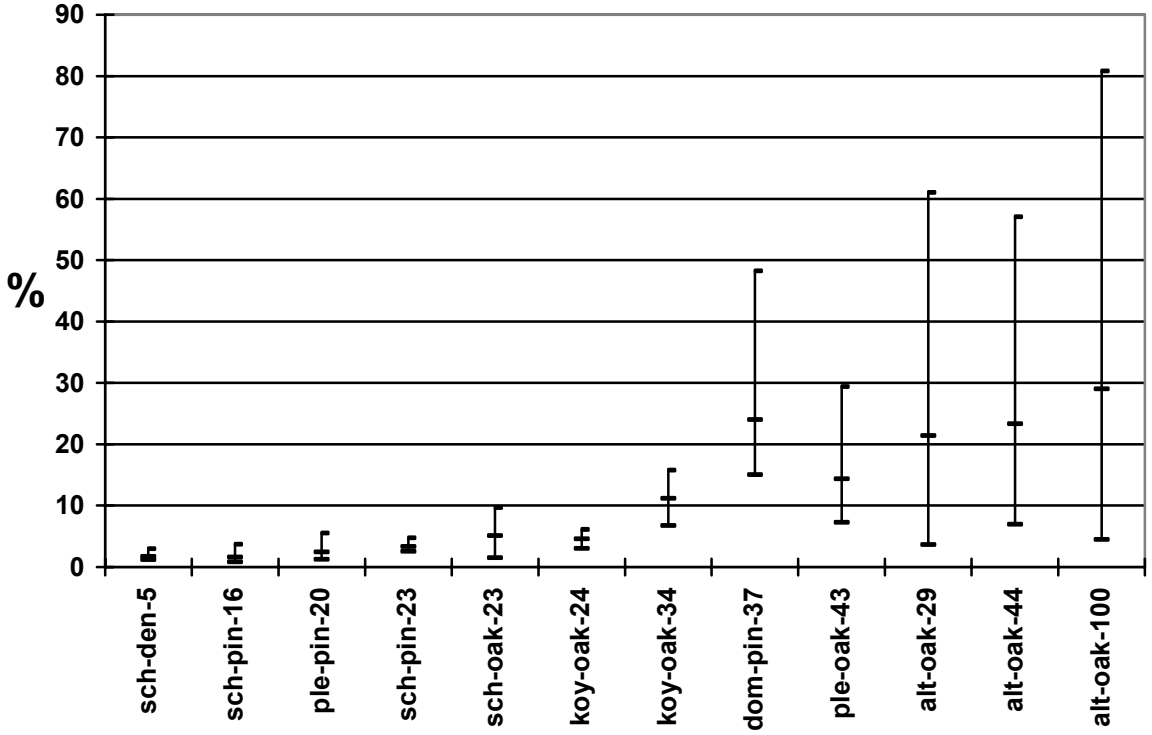


Figure 16: Percent mass loss on ignition in the afforested sites, youngest sites to the left and reference sites to the right of the x-axis, minimum, mean and maximum values.

Deviation is least in the youngest sites. With continuing accumulation of organic matter, variance increases rapidly after about 35 to 40 years. Litter is dispersed heterogeneously in **sch-oak-23**, with hardly any litter at sup-sample A/B and litter accumulation at E/F. Hence, empirical variance of organic matter content is larger than at other young sites (tab. 2). Older sites show a higher deviation, indicating a heterogeneity and variety of microhabitats at older sites.

Table 2: loss on ignition (%) of afforested sites, minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-den-5	1,19	3,00	1,72	0,50	21,00
sch-pin-16	0,84	3,69	1,60	0,78	12,00
ple-pin-20	1,26	5,54	2,43	1,56	11,00
sch-pin-23	2,57	4,74	3,35	0,69	12,00
sch-oak-23	1,52	9,68	5,11	2,73	12,00
koy-oak-24	3,01	6,10	4,62	1,09	12,00
koy-oak-34	6,71	15,74	11,18	2,89	12,00
dom-pin-37	15,03	48,26	24,03	9,33	18,00
ple-oak-43	7,26	29,39	14,35	7,82	12,00
alt-oak-29	3,63	61,01	21,39	15,03	24,00
alt-oak-44	6,96	57,06	23,31	12,94	36,00
alt-oak-100	4,47	80,80	29,02	24,05	43,00

4.1.1.3 Conductivity

Conductivity is significantly positively correlated to all tested soil properties (r = 0.7 to 0.9, p < 0.009 to 0.000) but pH, which is negatively correlated (r = -0.6, p < 0.045) and phosphate which is not correlated (r = 0.4, p < 0.212; tab. 9). The recently meliorated site **sch-den-5** shows higher conductivity than sites which have already suffered some weathering (fig. 17). Conductivity seems to be highly influenced by melioration during the first years. Later, litter accumulation (humic acids) seems to become the most important factor.

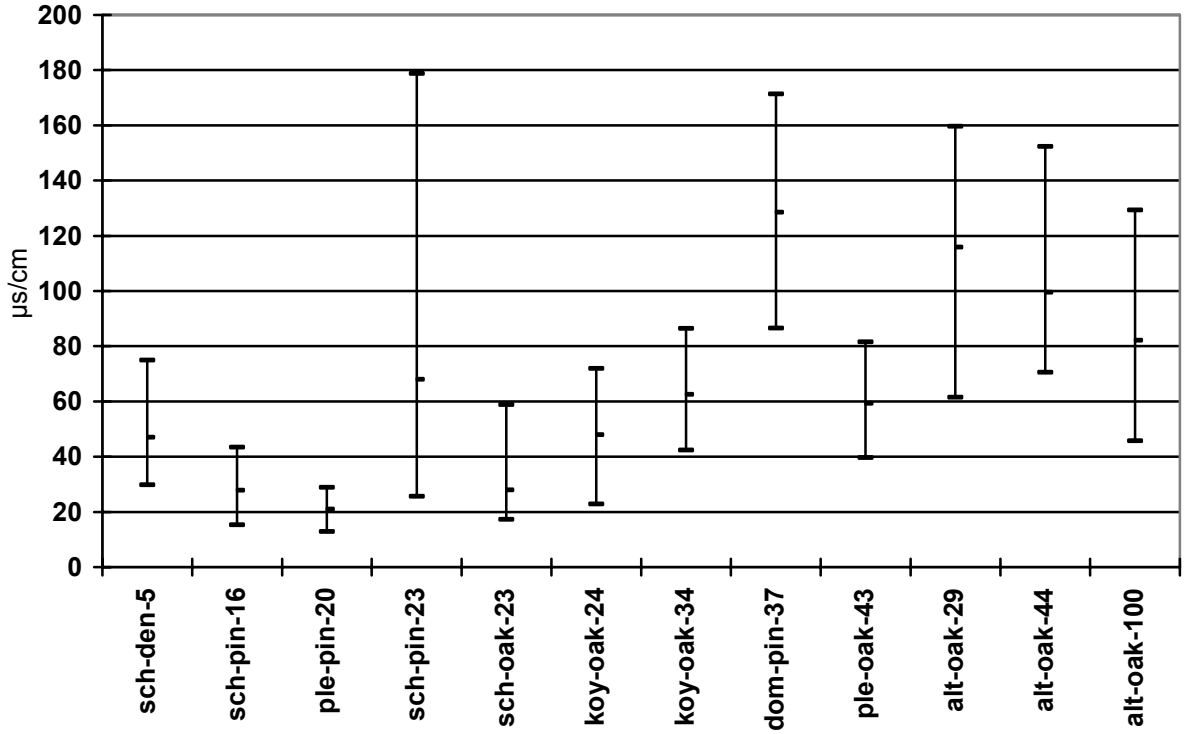


Figure 17: Conductivity of afforested sites, µs/cm, youngest sites to the left and reference sites to the right of the x-axis, minimum, mean and maximum values.

Generally, deviation increases with age. **Sch-pin-23** shows highest deviation, indicating high heterogeneity of its soil, similar to **dom-pin-37** which has the highest mean conductivity.

Table 3: Conductivity of afforested sites, µs/cm, minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-den-5	29,80	74,90	47,03	12,69	20,00
sch-pin-16	15,30	43,40	27,80	8,81	12,00
ple-pin-20	12,90	28,90	20,94	5,40	12,00
sch-pin-23	25,60	178,80	68,00	52,28	12,00
sch-oak-23	17,30	58,80	27,95	14,18	12,00

	min.	max.	mean	deviation	n
koy-oak-24	22,90	71,90	47,92	17,62	12,00
koy-oak-34	42,40	86,40	62,56	17,54	12,00
dom-pin-37	86,60	171,30	128,53	32,54	12,00
ple-oak-43	39,70	81,50	59,32	14,35	12,00
alt-oak-29	61,50	159,60	115,92	37,50	12,00
alt-oak-44	70,50	152,30	99,57	26,94	12,00
alt-oak-100	45,70	129,40	82,10	31,43	12,00

4.1.1.4 Water content

Water content shows highest positive correlations to stand age and conductivity (r = 0.9, p < 0.000), water capacity (r = 1, p < 0.000), ammonium and structure (r = 0.8, p < 0.001; tab. 9). However, the ash-meliorated soil at **dom-pin-37** shows the highest mean value (39.18 %), quite similar to conductivity. Water content of **ple-oak-43** is about as low as the 20 years younger oak afforestation **koy-oak-24** (fig. 18). There are no results for **sch-den-5**.

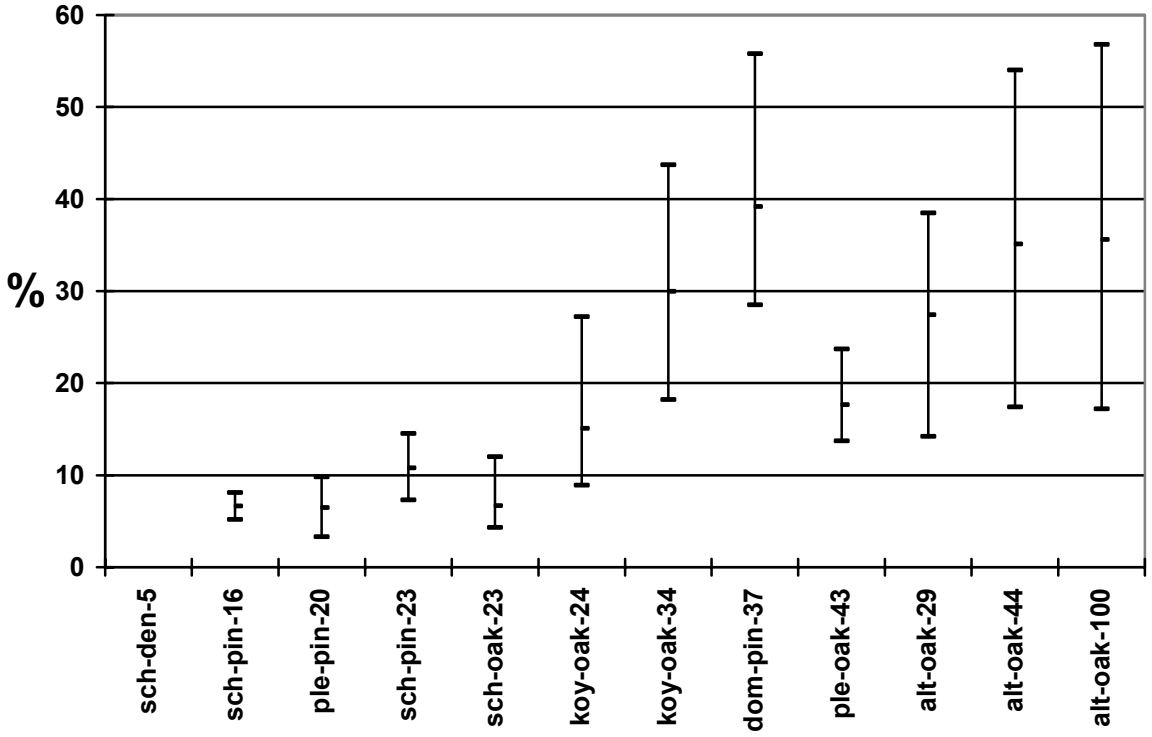


Figure 18: Water content of afforested sites (%), youngest sites to the left and reference sites to the right of the x-axis, minimum, mean and maximum values.

Deviation is highest at the two oldest reference sites **alt-oak-44** and **alt-oak-100**.

Table 4: Water content of afforested sites (%), minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-den-5	-	-	-	-	0,00
sch-pin-16	5,20	8,10	6,64	0,88	12,00
ple-pin-20	3,30	9,80	6,47	2,13	12,00
sch-pin-23	7,30	14,50	10,79	2,27	12,00
sch-oak-23	4,30	12,00	6,68	2,52	12,00
koy-oak-24	8,90	27,20	15,08	6,81	12,00
koy-oak-34	18,20	43,70	29,95	9,68	12,00
dom-pin-37	28,50	55,80	39,18	9,01	12,00
ple-oak-43	13,70	23,70	17,66	3,21	12,00
alt-oak-29	14,20	38,50	27,44	7,65	12,00
alt-oak-44	17,40	54,00	35,12	12,92	12,00
alt-oak-100	17,20	56,80	35,61	13,44	12,00

4.1.1.5 Water capacity

Increase of water capacity is also significantly correlated to stand age and structure ($r = 0.9$, $p < 0.000$ each), representing the highest possible correlation between organic matter content and water capacity ($r = 1$, $p < 0.000$). Other parameters are also positively correlated but pH which is negatively ($r = -0.7$, $p < 0.019$) correlated. To phosphate it shows no significant correlation ($r = -0.4$, $p < 0.225$; tab. 9). Mean water capacity increases until it shows a value at **dom-pin-37** similar to that of the 3 reference sites. **Ple-oak-43** again shows similar properties as **koy-oak-24** (fig. 19).

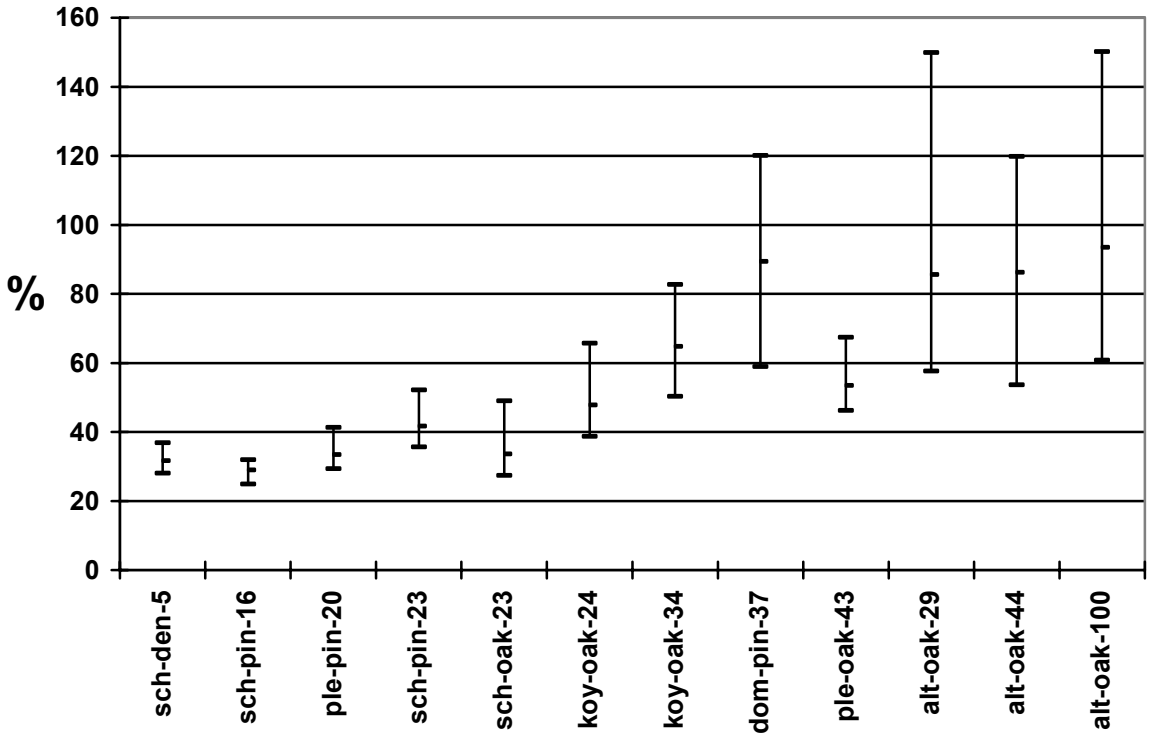


Figure 19: Water capacity of afforested sites (%), youngest sites to the left and reference sites to the right of the x-axis, minimum, mean and maximum values.

Deviation is again highest at the oldest sites, indicating their heterogeneity (tab. 5).

Table 5: Water capacity of afforested sites (%), minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-den-5	28,00	36,80	31,66	2,65	20,00
sch-pin-16	24,90	31,90	28,92	2,37	12,00
ple-pin-20	29,30	41,30	33,45	4,07	12,00
sch-pin-23	35,60	52,20	41,67	5,86	12,00
sch-oak-23	27,40	49,00	33,61	7,21	12,00
koy-oak-24	38,70	65,70	47,75	10,42	12,00
koy-oak-34	50,30	82,70	64,77	11,17	12,00
dom-pin-37	58,90	120,10	89,40	22,03	12,00
ple-oak-43	46,20	67,40	53,43	6,14	12,00
alt-oak-29	57,60	149,90	85,58	34,45	12,00
alt-oak-44	53,60	119,80	86,21	25,27	12,00
alt-oak-100	60,80	150,20	93,42	28,78	12,00

4.1.1.6 Phosphate

There is only a significantly positive correlation between phosphate and pH ($r = 0.7$, $p < 0.019$; tab. 9). This is mainly due to the high content of phosphate in the recently meliorated site **sch-den-5** (2.22 mg/100g in the mean, tab. 6). The reference sites show lowest values for phosphate (fig.20).

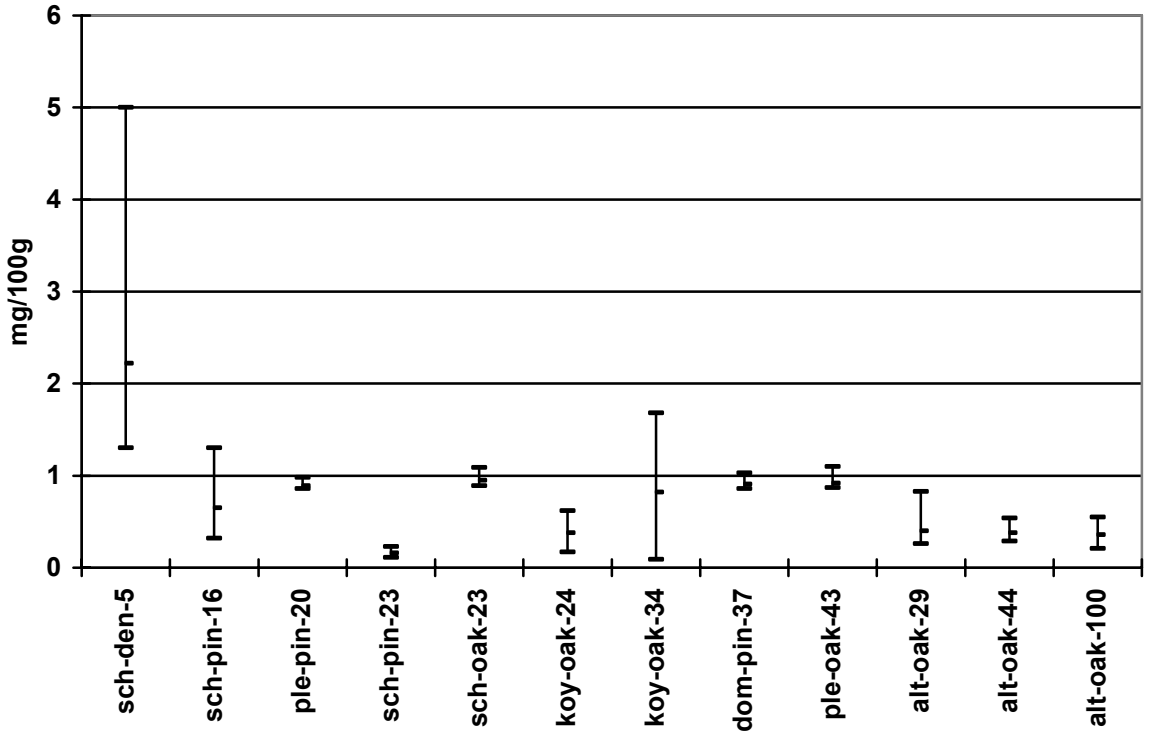


Figure 20: Phosphate in the afforested sites (mg/100g), youngest sites to the left and reference sites to the right of the x-axis, minimum, mean and maximum values.

Deviation is highest at the youngest sites, where weathering is still in process. In addition, **koy-oak-34** also shows high deviation. However, there is no immediate explanation at hand for this observation.

Table 6: Phosphate in the afforested sites (mg/100g), minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-den-5	1,30	5,00	2,22	0,87	20,00
sch-pin-16	0,32	1,30	0,65	0,34	12,00
ple-pin-20	0,86	0,98	0,89	0,04	12,00
sch-pin-23	0,11	0,23	0,16	0,04	12,00
sch-oak-23	0,89	1,09	0,95	0,06	12,00
koy-oak-24	0,17	0,62	0,38	0,16	12,00
koy-oak-34	0,09	1,68	0,82	0,54	12,00

	min.	max.	mean	deviation	n
dom-pin-37	0,86	1,03	0,91	0,05	12,00
ple-oak-43	0,87	1,10	0,92	0,07	12,00
alt-oak-29	0,26	0,83	0,40	0,19	12,00
alt-oak-44	0,29	0,54	0,38	0,09	12,00
alt-oak-100	0,21	0,55	0,36	0,12	12,00

4.1.1.7 Ammonium

Ammonium shows significantly positive correlations to structure, stand age and water capacity ($r = 0.9$, $p < 0.000$ each), to water content and organic matter content ($r = 0.8$, $p < 0.001$ each) and conductivity ($r = 0.7$, $p < 0.008$; tab. 9). Ammonium can be considered as an indirect proof for biological activities in soils. Taken this into account, then there is only at the oak-afforested sites **koy-oak-34** and **ple-oak-43** a biological activity on reclaimed land comparable to the youngest reference site. Biological activity is highest at the 2 oldest reference sites. **Sch-den-5** with its dense herb layer also shows higher activity than the young pine afforestations with hardly any litter layer (fig. 21).

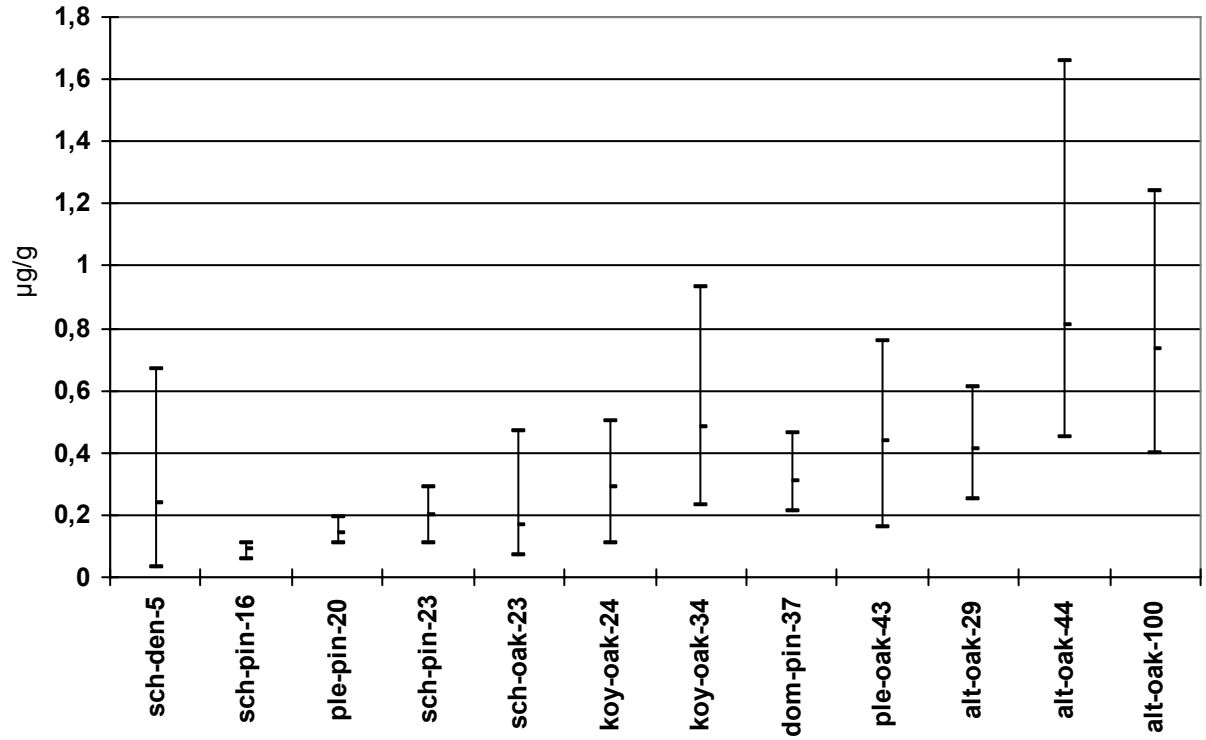


Figure 21: Ammonium in afforested sites (µg/g), youngest sites to the left and reference sites to the right of the x-axis, minimum, mean and maximum values.

Deviation is highest at those soils with highest biological activity, which are the 2 oldest reference sites and the youngest site. Oak-afforestations seem to show higher deviation than pine afforestations of the same age, especially if one looks at **sch-pin-23** and **dom-pin-37**.

Table 7: Ammonium in afforested sites (µs/cm), minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-den-5	0,03	0,67	0,24	0,23	14,00
sch-pin-16	0,06	0,11	0,09	0,02	12,00
ple-pin-20	0,11	0,19	0,14	0,03	12,00
sch-pin-23	0,11	0,29	0,20	0,05	12,00
sch-oak-23	0,07	0,47	0,17	0,12	12,00
koy-oak-24	0,11	0,50	0,29	0,13	12,00
koy-oak-34	0,23	0,93	0,48	0,20	12,00
dom-pin-37	0,21	0,46	0,31	0,08	12,00
ple-oak-43	0,16	0,76	0,44	0,18	12,00
alt-oak-29	0,25	0,61	0,41	0,12	12,00
alt-oak-44	0,45	1,66	0,81	0,44	12,00
alt-oak-100	0,40	1,24	0,73	0,29	12,00

4.1.1.8 Nitrate

Nitrate shows positive correlation to conductivity ($r = 0.9$, $p < 0.001$), water capacity ($r = 0.7$, $p < 0.013$), organic matter content ($r = 0.7$, $p < 0.022$), stand age ($r = 0.7$, $p < 0.030$) and structure ($r = 0.6$, $p < 0.050$; tab. 9). It is negatively correlated to pH ($r = -0.6$, $p < 0.007$; tab. 9). Highest nitrate content has the ash-meliorated soil at **dom-pin-37**, which is about 2 to 3 times higher than at the other sites (tab. 8). If **dom-pin-37** is excluded, the negative correlation between pH and nitrate is even stronger ($r = -0.8$, $p < 0.003$) and a negative correlation to phosphate occurs ($r = -0.7$, $p < 0.021$) but correlation to organic matter content is no longer significant ($r = 0.5$, $p < 0.121$). There are no results for **ple-pin-20** (fig. 22).

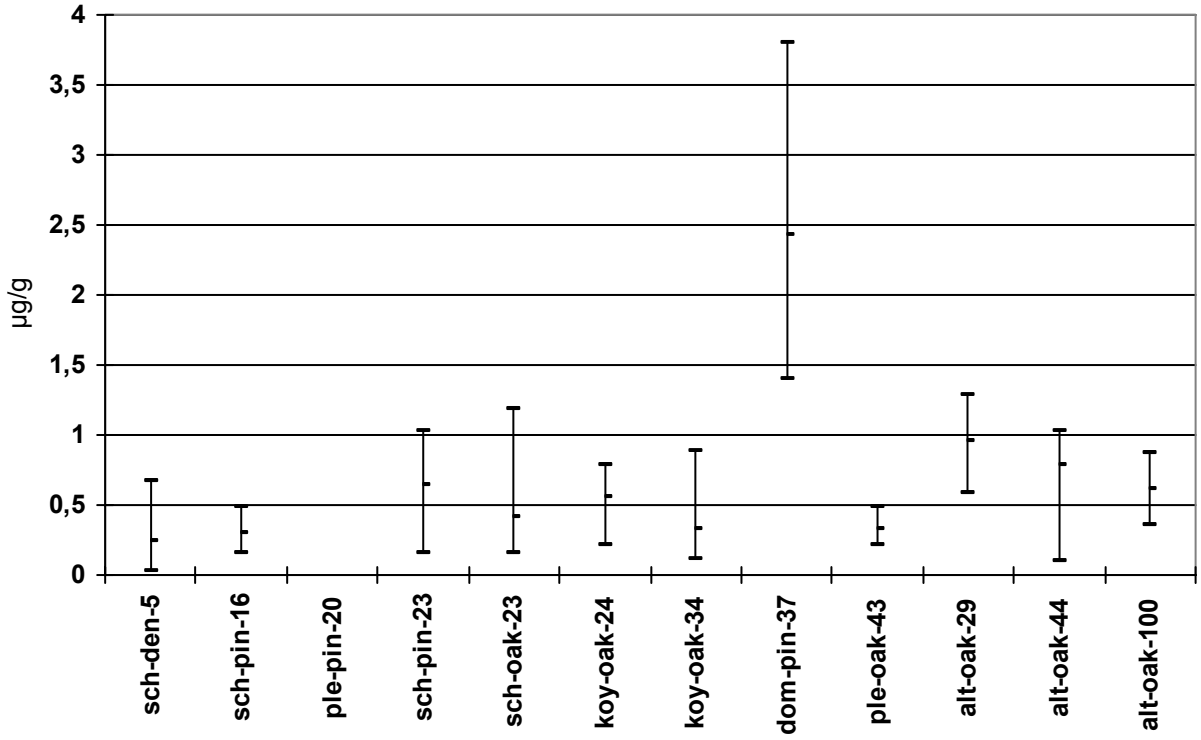


Figure 22: Nitrate in afforested sites (µg/g), youngest sites to the left and reference sites to the right of the x-axis, minimum, mean and maximum values.

Deviation is highest at the ash-meliorated site **dom-pin-37** with its highest content of nitrate.

Table 8: Nitrate in afforested sites (µg/g), minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-den-5	0,03	0,67	0,24	0,23	14,00
sch-pin-16	0,16	0,48	0,30	0,10	12,00
ple-pin-20	-	-	-	-	0,00
sch-pin-23	0,16	1,03	0,64	0,29	12,00
sch-oak-23	0,16	1,19	0,42	0,32	12,00
koy-oak-24	0,22	0,78	0,56	0,17	12,00
koy-oak-34	0,11	0,88	0,33	0,20	12,00
dom-pin-37	1,40	3,80	2,43	0,73	12,00
ple-oak-43	0,21	0,49	0,33	0,09	12,00
alt-oak-29	0,59	1,28	0,96	0,19	12,00
alt-oak-44	0,10	1,03	0,78	0,24	12,00
alt-oak-100	0,36	0,87	0,61	0,15	12,00

Table 9: Correlations between soil properties, significant negative correlations blue, significant positive correlations orange (Spearman-Rho).

forest	pH		Conductivity		Water content		Water capacity		Phosphate		Ammonium		Nitrate		Organic matter content		Structure		Stand age
Spearman-Rho	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r
pH	1,0																		
Conductivity	-0,6	0,045	1,0																
Water content	-0,5	0,136	0,9	0,000	1,0														
Water capacity	-0,7	0,019	0,9	0,000	1,0	0,000	1,0												
Phosphate	0,7	0,007	-0,4	0,212	-0,2	0,592	-0,4	0,225	1,0										
Ammonium	-0,6	0,058	0,7	0,008	0,8	0,001	0,9	0,000	-0,3	0,378	1,0								
Nitrate	-0,6	0,007	0,9	0,000	0,6	0,066	0,7	0,013	-0,5	0,119	0,4	0,290	1,0						
Organic matter content	-0,6	0,042	0,8	0,001	0,9	0,000	1,0	0,000	-0,2	0,463	0,8	0,001	0,7	0,022	1,0				
Structure	-0,7	0,014	0,8	0,005	0,8	0,001	0,9	0,000	-0,4	0,212	0,9	0,000	0,6	0,050	0,9	0,000	1,0		
Stand age	-0,6	0,059	0,7	0,009	0,9	0,000	0,9	0,000	-0,3	0,269	0,9	0,000	0,7	0,030	0,9	0,000	1,0	0,000	1,0

4.1.1.9 Cluster analysis

Cluster analysis for all soil properties separates 2 main groups: the reference sites plus the ash-meliorated soil at **dom-pin-37** are separated from the reclamation sites. This is probably due to their high organic matter content. The reclamation sites are further subdivided into a group of 3 younger sites (**ple-pin-20**, **sch-oak-23**, **sch-pin-16**) and the other sites, varying from the youngest to the oldest site (fig. 23).

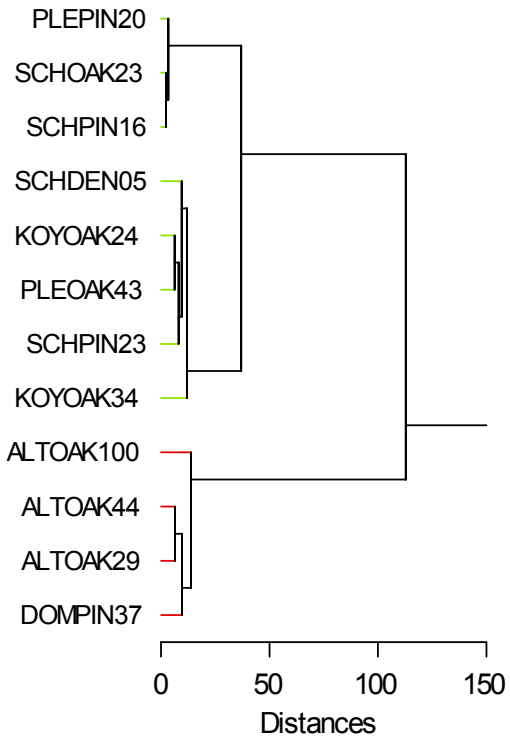


Figure 23: Cluster analysis of soil parameters (distance metric is Euclidian, Ward minimum variance method).

Table 10: Clustering of afforestation sites.

Cluster containing	and Cluster containing	were joined at a distance	No of members in new cluster
SCHOAK23	SCHPIN16	2.163	2
PLEPIN20	SCHOAK23	3.278	3
PLEOAK43	KOYOAK24	6.114	2
ALTOAK44	ALTOAK29	6.531	2
SCHPIN23	PLEOAK43	7.796	3
ALTOAK44	DOMPIN37	9.470	3
SCHDEN5	SCHPIN23	9.480	4
SCHDEN5	KOYOAK43	11.891	5
ALTOAK44	ALTOAK100	14.098	4
PLEPIN20	SCHDEN5	36.341	8
PLEPIN20	ALTOAK44	112.493	12

4.1.2 Chronosequence 2: Sites of free succession

Sites of free succession were arranged after structure and age (for the arrangement see chapter 3.6).

4.1.2.1 pH

pH differs from 2.7 (**sch-bar-4**) to 7.8 (**sch-spa-16**), and is positively correlated to conductivity ($r = 0.7$, $p < 0.000$, tab. 19). There are no other significant correlations, but pH certainly depends on original soil properties and melioration, which complicates the interpretation somewhat. Just after melioration, pH is generally high and decreases after weathering and elution. Non-meliorated sites with mixed tertiary and quaternary substrate show lowest pH from the very beginning (**scha-bar-4**). Sites of the same age but meliorated (**cot-spa-4**) show considerably higher pH (7.0 – 7.7). Due to the buffering-properties of lignite-ash, the ash-meliorated site **sch-den-23** also shows a rather high pH-value (7.5). Sites with a large amount of lime or loan in the quaternary material (some sites in Schlabendorf-Süd; Plessa) can still be recognized after dumping by high maximum pH (e.g. **sch-spa-16**; **sch-den-16**; fig.24).

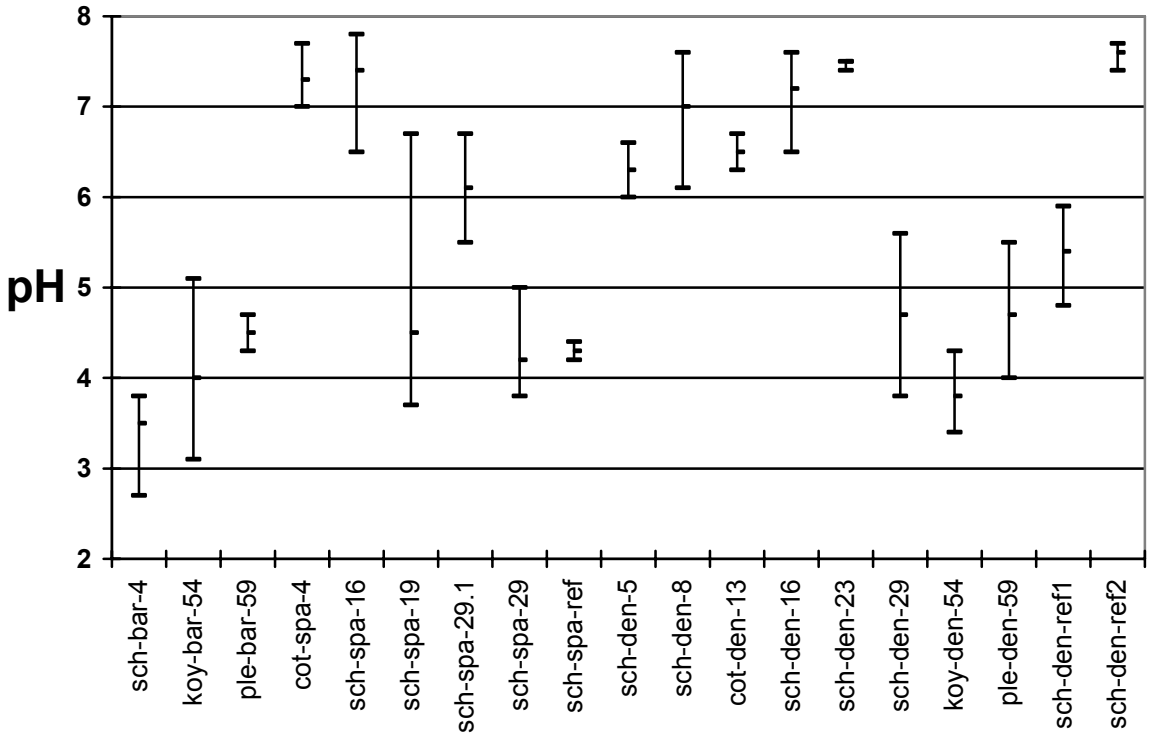


Figure 24: pH of open sites; maximal, minimal and mean values; sites distinguished between vegetation structure and age from left to right: bare substrate, sparse vegetation and dense vegetation.

Deviation is least at the carefully meliorated agricultural ash-soil of **sch-den-23** and the reference sites **sch-spa-ref** and **sch-den-ref2**, although variance is already 10 to 20 times higher at the undisturbed reference sites than that of the carefully ash-meliorated one. Highest empirical variances have the sites where pyrite-containing tertiary substrate was mixed with loam/lime-containing quaternary substrate (**sch-spa-19**, tab. 11).

Table 11: pH of sites with free succession, minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-bar-4	2,7	3,8	3,5	0,31	20,00
koy-bar-54	3,1	5,1	4,0	0,74	12,00
ple-bar-59	4,3	4,7	4,5	0,12	12,00
cot-spa-4	7,0	7,7	7,3	0,25	12,00
sch-spa-16	6,5	7,8	7,4	0,31	20,00
sch-spa-19	3,7	6,7	4,5	0,88	20,00
sch-spa-29	5,5	6,7	6,1	0,42	12,00
sch-spa-29.1	3,8	5,0	4,2	0,40	12,00
sch-spa-ref	4,2	4,4	4,3	0,08	12,00
sch-den-5	6,0	6,6	6,3	0,15	20,00
sch-den-8	6,1	7,6	7,0	0,63	12,00
cot-den-13	6,3	6,7	6,5	0,14	12,00
sch-den-16	6,5	7,6	7,2	0,36	12,00
sch-den-23	7,4	7,5	7,5	0,03	12,00
sch-den-29	3,8	5,6	4,7	0,70	12,00
koy-den-54	3,4	4,3	3,8	0,30	12,00
ple-den-59	4,0	5,5	4,7	0,57	12,00
sch-den-ref1	4,8	5,9	5,4	0,35	20,00
sch-den-ref2	7,4	7,7	7,6	0,10	20,00

4.1.2.2 Organic matter content

Organic matter content is significantly positively correlated to structure ($r = 0.7$, $p < 0.001$) but there is no correlation to site age ($r = 0.3$, $p < 0.196$). Organic matter content is dependent on vegetational structure and its age, the remains of coal in the soil, content of lime and melioration practise. Generally, it increases with the vegetational structure. Humus accumulates after an adequate vegetation structure is established. Therefore, it is positively correlated to plant relevant parameters like conductivity ($r = 0.6$, $p < 0.003$), water content ($r = 0.8$, $p < 0.000$), water capacity, ammonium and nitrate ($r = 0.7$, $p < 0.002$ each). However, organic matter content is not correlated to phosphate ($r = 0.3$, $p < 0.273$; tab. 19), indicating that nitrogen is the limiting factor for plant growth and not phosphate. Sites with dense vegetation have higher organic matter contents than bare sites or those with sparse vegetation and therefore hardly any litter layers or root penetration. Outliers like **sch-bar-5, koy-bar-54** and **koy-den-54** have high amounts of remaining coal or were meliorated with ashes like **sch-den-23**. Other outliers are due to methodical deficiencies: During

incineration, not only humus vanishes, but also lime. Therefore, lime containing sites like **sch-den-16** or **sch-den-ref2** also show a high reduction of weight (fig. 25).

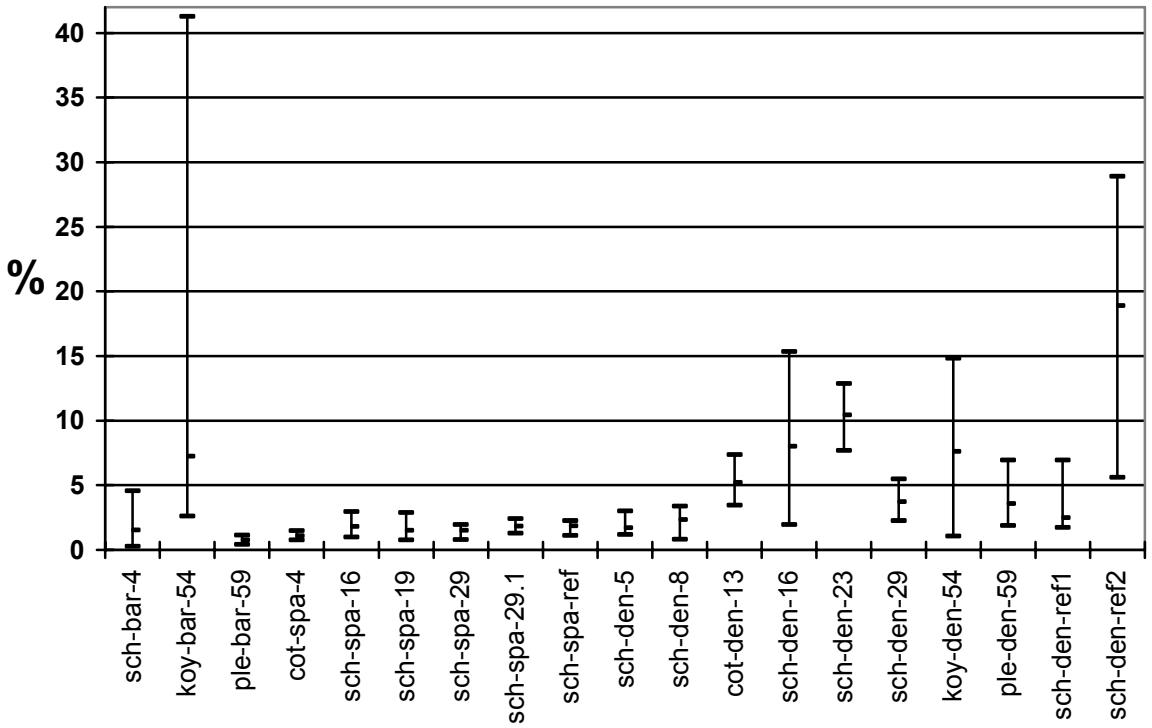


Figure 25: Organic matter content (%) in sites of free succession; maximal, minimal and mean values; sites distinguished between vegetation structure and age from left to right: bare substrate, sparse vegetation and dense vegetation.

Least deviation is found at sites with low organic matter content: **ple-bar-59, cot-spa-4** and **sch-spa-ref**. High variance at sites with sparse or no vegetation indicates a high amount of remaining coal (**koy-bar-54**). At other sites with known lime content, it indicates the reduction of weight due to lime incineration, which adds to the incineration of organic matter content (fig. 25; tab. 12).

Table 12: Organic matter content (%) of sites with free succession, minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-bar-4	0,28	4,57	1,53	1,19	25,00
koy-bar-54	2,61	41,27	7,24	11,00	12,00
ple-bar-59	0,41	1,14	0,77	0,23	14,00
cot-spa-4	0,76	1,48	1,08	0,28	12,00
sch-spa-16	0,98	2,96	1,80	0,60	31,00
sch-spa-19	0,78	2,87	1,51	0,48	19,00
sch-spa-29	0,79	1,97	1,51	0,43	12,00
sch-spa-29.1	1,28	2,41	1,84	0,35	12,00
sch-spa-ref	1,12	2,26	1,85	0,32	12,00
sch-den-5	1,19	3,00	1,72	0,50	21,00

	min.	max.	mean	deviation	n
sch-den-8	0,83	3,37	2,33	0,86	12,00
cot-den-13	3,44	7,37	5,21	1,02	12,00
sch-den-16	1,96	15,34	8,00	5,99	12,00
sch-den-23	7,68	12,88	10,45	1,54	12,00
sch-den-29	2,25	5,48	3,71	1,10	12,00
koy-den-54	1,06	14,83	7,61	4,26	12,00
ple-den-59	1,88	6,95	3,56	1,57	12,00
sch-den-ref1	1,74	6,95	2,49	1,18	17,00
sch-den-ref2	5,61	28,91	18,89	7,37	21,00

4.1.2.3 Conductivity

Conductivity is not correlated to structure (r = 0.4, p< 0.090) or site age (r = -0.3, p < 0.204). However, it is correlated to organic matter content and it is also weakly positively correlated to conductivity (r = 0.6, p = < 0.003), indicating the importance of ions for plant growth, and water capacity (r = 0.5, p < 0.030) and water content (r = 0.6, p < 0.007; tab. 19). Conductivity is highest at the ash-meliorated site **sch-den-23**, the lime containing reference site **sch-den-ref2** and the littoral site **sch-den-8**, which is influenced by the rising groundwater table. Lowest conductivity shows the oldest dune **ple-bar-59** and the reference site **sch-spa-ref** (fig. 26).

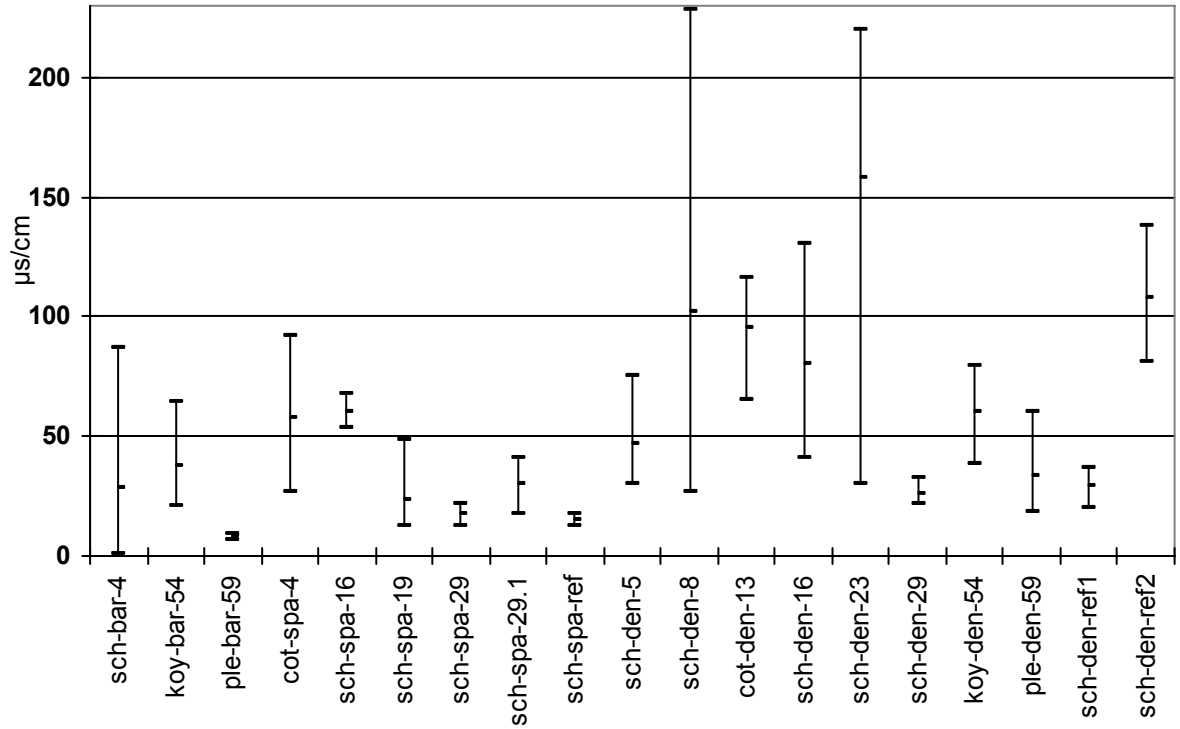


Figure 26: Conductivity (µs/cm) in sites of free succession; maximal, minimal and mean values; sites distinguished between vegetation structure and age from left to right: bare substrate, sparse vegetation and dense vegetation.

Deviation is least at the poor reference site **sch-spa-ref** and the bare site **ple-bar-59**. Highest deviation shows the littoral site **sch-den-8**, reflecting the heterogeneity caused by ground water influence, and the ash-meliorated site **sch-den-23**. Recently meliorated sites like **cot-spa-4** or lignite containing sites like **sch-bar-4** and **koy-bar-54** also show comparably high deviation (fig. 26, tab.13).

Table 13: Conductivity (µs/cm) of sites with free succession, minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-bar-4	1,10	87,00	28,23	21,51	20,00
koy-bar-54	20,50	64,00	37,59	15,88	12,00
ple-bar-59	6,70	9,50	8,47	0,92	12,00
cot-spa-4	27,00	91,70	58,03	21,00	12,00
sch-spa-16	53,80	67,80	60,13	4,85	20,00
sch-spa-19	12,90	48,70	23,69	11,48	20,00
sch-spa-29	12,90	21,40	17,50	2,84	12,00
sch-spa-29.1	17,50	40,90	30,12	7,76	12,00
sch-spa-ref	12,40	17,30	15,03	1,56	12,00
sch-den-5	29,80	74,90	47,03	12,69	20,00
sch-den-8	27,00	228,00	101,67	68,13	12,00
cot-den-13	65,10	116,20	95,68	18,69	12,00
sch-den-16	40,60	130,60	80,43	35,05	12,00
sch-den-23	30,00	220,00	158,33	71,58	12,00
sch-den-29	21,90	32,80	26,21	3,26	12,00
koy-den-54	38,80	79,40	59,82	17,27	12,00
ple-den-59	18,20	60,10	33,22	14,38	12,00
sch-den-ref1	20,10	36,70	29,23	4,68	20,00
sch-den-ref2	80,80	137,90	107,83	17,94	20,00

4.1.2.4 Water content

Water content shows highest positive correlation to organic matter content ($r = 0.8$, $p < 0.000$). Furthermore, it is positively correlated to structure ($r = 0.6$, $p < 0.011$), ammonium and nitrate ($r = 0.6$, $p < 0.013$ each) and water capacity ($r = 0.6$, $p < 0.018$; tab. 19). Sites with a high content of remaining lignite like koy-bar-54 and koy-den-54 have comparably high water content, same as the ash-meliorated site sch-den-23 (fig. 27). There are no data for **sch-den-5**.

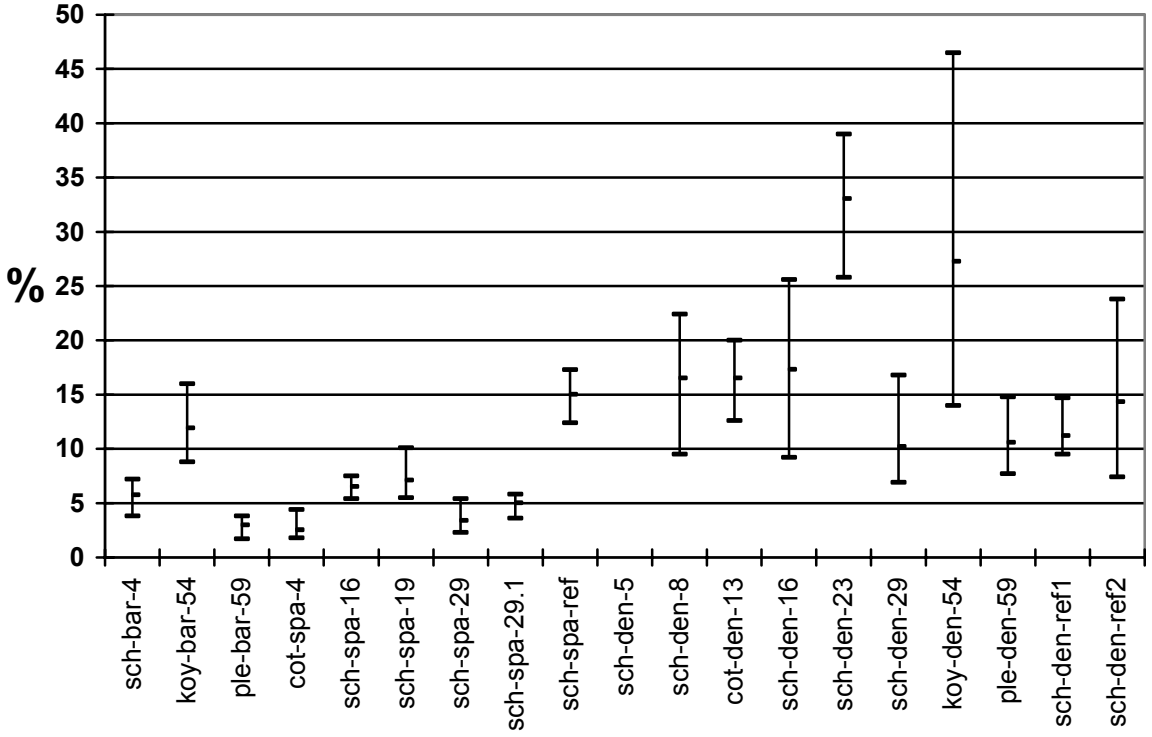


Figure 27: Water content (%) in sites of free succession; maximal, minimal and mean values; sites distinguished between vegetation structure and age from left to right: bare substrate, sparse vegetation and dense vegetation.

Deviation increases with increasing organic matter content. Sites with remaining lignite, like **sch-bar-4**, **koy-bar-54** or **koy-den-54**, show higher deviation than comparable sites of the same structure (fig. 27, tab. 14).

Table 14: Water content (%) of sites with free succession, minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-bar-4	3,80	7,20	5,75	0,81	20,00
koy-bar-54	8,80	16,00	11,92	2,46	12,00
ple-bar-59	1,70	3,80	2,97	0,76	12,00
cot-spa-4	1,80	4,40	2,53	0,92	12,00
sch-spa-16	5,40	7,50	6,52	0,56	20,00
sch-spa-19	5,50	10,10	7,11	1,43	20,00
sch-spa-29	2,30	5,40	3,39	0,84	12,00
sch-spa-29.1	3,60	5,80	5,03	0,78	12,00
sch-spa-ref	12,40	17,30	15,03	1,56	12,00
sch-den-5	-	-	-	-	0,00
sch-den-8	9,50	22,40	16,53	4,64	12,00
cot-den-13	12,60	20,00	16,54	2,88	12,00
sch-den-16	9,20	25,60	17,32	5,19	12,00
sch-den-23	25,80	39,00	33,05	4,12	12,00
sch-den-29	6,90	16,80	10,21	3,55	12,00
koy-den-54	14,00	46,50	27,28	10,31	12,00

	min.	max.	mean	deviation	n
ple-den-59	7,70	14,80	10,59	2,28	12,00
sch-den-ref1	9,50	14,70	11,22	1,46	20,00
sch-den-ref2	7,40	23,80	14,33	4,48	20,00

4.1.2.5 Water capacity

Like water content, maximum water capacity is positively correlated to organic matter content ($r = 0.7$, $p < 0.002$, tab. 19). Again, lignite containing sites (**sch-bar-4**, **koy-bar-54** and **koy-den-54**) and the ash-meliorated site **sch-den-23** show highest values. The measured parameters do not offer an explanation for the high water capacity of **sch-spa-16** (fig. 28). This might be due to the mixture of sandy and loamy materials. As organic matter content and structure are closely related in the chronosequence, water capacity is also correlated to structure ($r = 0.6$, $p < 0.005$) and the nutrients phosphate ($r = 0.5$, $p < 0.029$), ammonium and nitrate ($r = 0.5$, $p < 0.017$ each; tab. 15).

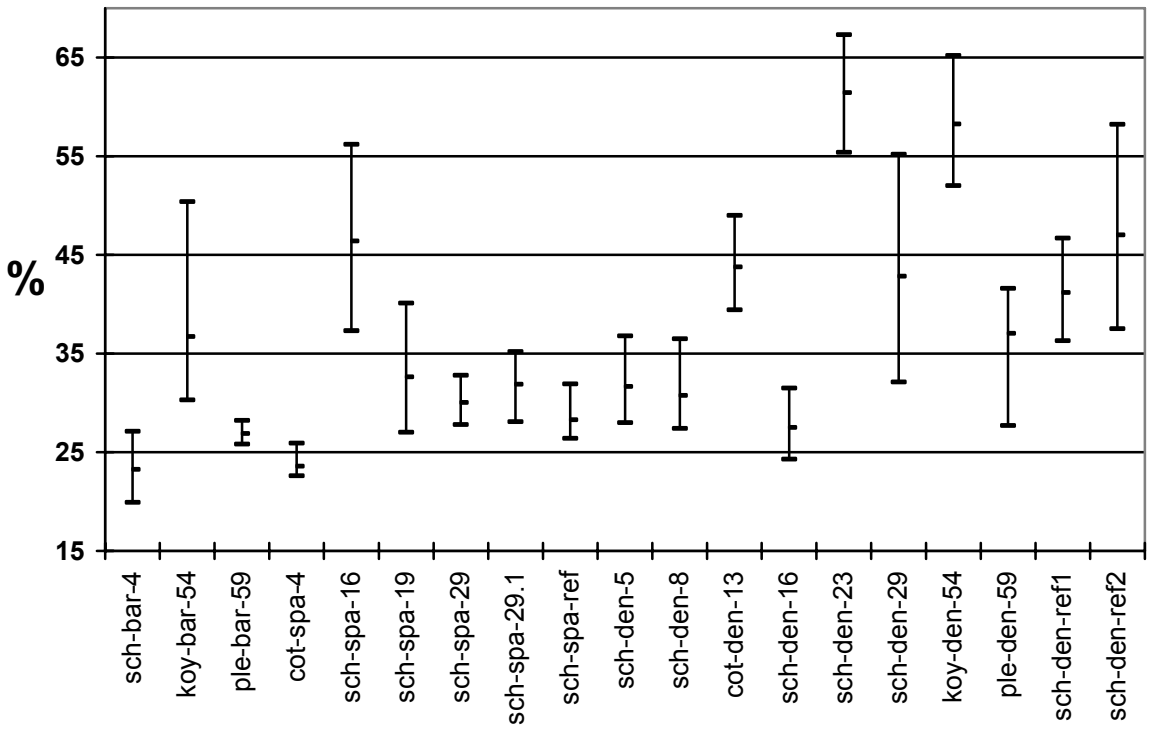


Figure 28: Maximal water capacity (%) in sites of free succession; maximal, minimal and mean values; sites distinguished between vegetation structure and age from left to right: bare substrate, sparse vegetation and dense vegetation.

Deviation is highest at the lignite containing site **koy-bar-54** and **sch-den-ref2**, where sandy soil and loamy soil make up heterogeneous soil conditions. Again, there are no explanations for the high deviation of **sch-spa-16** and **sch-den-29**at hand (fig 28, tab. 15).

Table 15: Maximal water capacity (%) of sites with free succession, minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-bar-4	19,90	27,10	23,26	1,83	20,00
koy-bar-54	30,30	50,40	36,73	6,35	12,00
ple-bar-59	25,80	28,20	26,88	0,83	12,00
cot-spa-4	22,60	25,90	23,56	1,05	12,00
sch-spa-16	37,30	56,20	46,41	6,41	12,00
sch-spa-19	27,00	40,10	32,63	3,59	20,00
sch-spa-29	27,80	32,80	30,03	1,51	12,00
sch-spa-29.1	28,10	35,20	31,89	2,15	12,00
sch-spa-ref	26,40	31,90	28,29	1,91	12,00
sch-den-5	28,00	36,80	31,66	2,65	20,00
sch-den-8	27,40	36,50	30,76	3,19	12,00
cot-den-13	39,40	49,00	43,76	3,40	12,00
sch-den-16	24,30	31,50	27,49	2,13	20,00
sch-den-23	55,40	67,30	61,43	4,14	12,00
sch-den-29	32,10	55,20	42,82	8,68	12,00
koy-den-54	52,00	65,20	58,25	4,24	12,00
ple-den-59	27,70	41,60	37,03	3,83	12,00
sch-den-ref1	36,30	46,70	41,17	2,55	20,00
sch-den-ref2	37,50	58,20	47,01	5,67	20,00

4.1.2.6 Phosphate

As an important nutrient, phosphate is positively correlated to structure ($r = 0.6$, $p < 0.005$) and water capacity ($r = 0.5$, $p < 0.029$). However, it is not correlated to organic matter content or other parameters (tab. 19). Highest mean values were found at the recently for afforestation meliorated site **sch-den-5** and **koy-den-54**. The second highest value was found at the for agriculture ash-meliorated site **sch-den-23** (fig. 29). Obviously, melioration determines the content of phosphate in these soils.

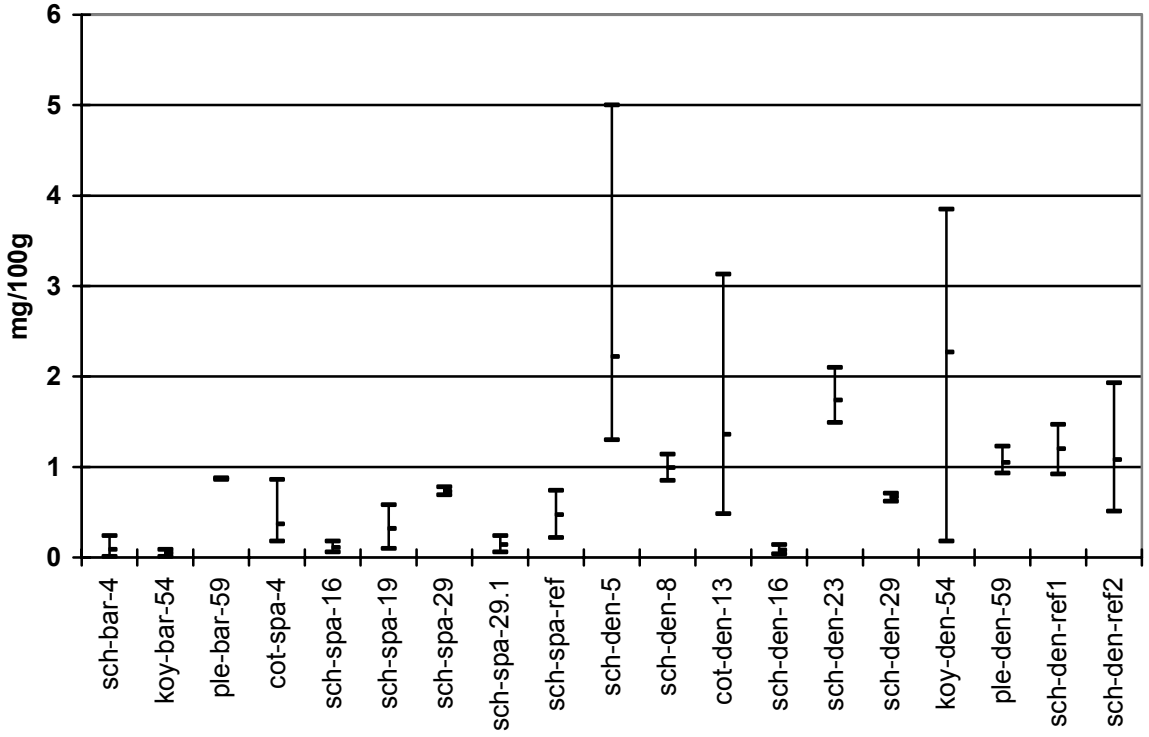


Figure 29: Phosphate (mg/100g) in sites of free succession; maximal, minimal and mean values; sites distinguished between vegetation structure and age from left to right: bare substrate, sparse vegetation and dense vegetation.

Deviation is highest at the 2 sites with maximal phosphate content. **Cot-den-13** also shows a high deviation. The subsamples D to F showed up to 3 times higher values than A to C. This is hard to explain, but there are sites in the PML where material for melioration is dumped before usage (like the “Kalkplatz” in Cottbus-Nord). This might offer some explanation for unusual high values of certain parameters on a small scale.

Table 16: Phosphate (mg/100g) of sites with free succession, minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-bar-4	0,01	0,24	0,09	0,06	20,00
koy-bar-54	0,01	0,09	0,05	0,03	12,00
ple-bar-59	0,86	0,88	0,87	0,01	12,00
cot-spa-4	0,18	0,86	0,37	0,25	12,00
sch-spa-16	0,06	0,18	0,11	0,04	12,00
sch-spa-19	0,10	0,58	0,32	0,16	20,00
sch-spa-29	0,69	0,78	0,73	0,03	12,00
sch-spa-29.1	0,06	0,24	0,14	0,06	12,00
sch-spa-ref	0,22	0,74	0,47	0,16	12,00
sch-den-5	1,30	5,00	2,22	0,87	20,00
sch-den-8	0,85	1,14	0,99	0,09	12,00
cot-den-13	0,48	3,13	1,36	9,03	12,00
sch-den-16	0,04	0,14	0,08	0,03	20,00

	min.	max.	mean	deviation	n
sch-den-23	1,49	2,10	1,74	0,24	12,00
sch-den-29	0,62	0,71	0,67	0,03	12,00
koy-den-54	0,18	3,85	2,27	1,11	12,00
ple-den-59	0,93	1,23	1,05	0,11	12,00
sch-den-ref1	0,92	1,47	1,20	0,16	20,00
sch-den-ref2	0,51	1,93	1,08	0,41	20,00

4.1.2.7 Ammonium

As an important nutrient, ammonium is positively related to structure ($r = 0.7$, $p < 0.000$), organic matter content ($r = 0.7$, $p < 0.002$) and the resulting effects on water content and water capacity ($r = 0.6$, $p < 0.013$ each). Both forms of nitrogen (ammonium and nitrate) are significantly correlated ($r = 0.7$, $p < 0.001$; tab. 19). Highest mean values are found at the littoral site **sch-den-8** and the 2 oldest reclamation sites with dense vegetation **koy-den-54** and **ple-den-59**. The bare sites **sch-bar-4** and **koy-bar-54** show relatively high values of ammonium (fig. 30). As ammonium is a product during the process of nitrification, it is an indirect measurement for the activity of the soil micro flora. It is interesting to notice that all sites with dense vegetation contain at least a mean value of 0.2 µg ammonium/g. This is also true for **sch-spa-29** which has been invaded to 2/3 by a dense *Calamagrostis epigejos* stand.

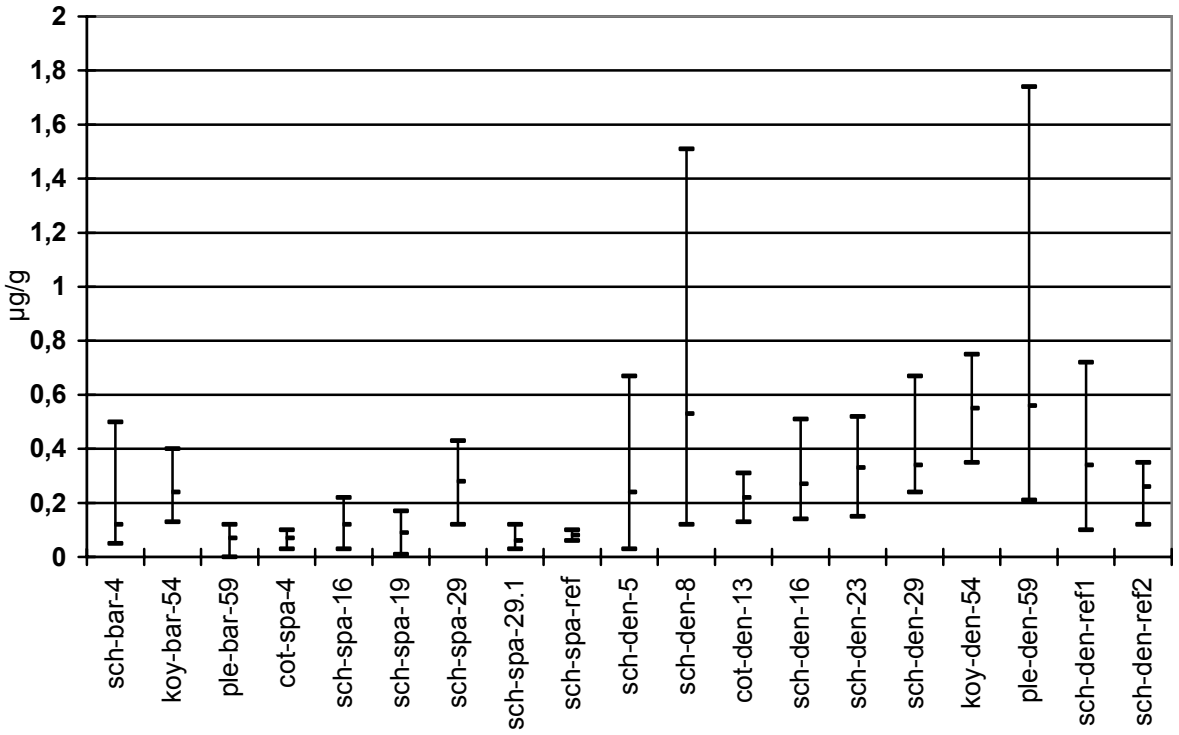


Figure 30: Ammonium (µg/g) in sites of free succession; maximal, minimal and mean values; sites distinguished between vegetation structure and age from left to right: bare substrate, sparse vegetation and dense vegetation.

Again we find highest deviation at the littoral site **sch-den-8** with its heterogeneous conditions and at the oldest reclamation site with dense vegetation **ple-den-59**, indicating complex soil conditions (tab. 17).

Table 17: Ammonium (µg/g) of sites with free succession, minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-bar-4	0,05	0,50	0,12	0,12	20,00
koy-bar-54	0,13	0,40	0,24	0,09	12,00
ple-bar-59	0,00	0,12	0,07	0,04	12,00
cot-spa-4	0,03	0,10	0,07	0,03	12,00
sch-spa-16	0,03	0,22	0,12	0,06	20,00
sch-spa-19	0,01	0,17	0,09	0,04	20,00
sch-spa-29	0,03	0,12	0,06	0,03	12,00
sch-spa-29.1	0,12	0,43	0,28	0,10	12,00
sch-spa-ref	0,06	0,10	0,08	0,01	12,00
sch-den-5	0,03	0,67	0,24	0,23	14,00
sch-den-8	0,12	1,51	0,53	0,51	12,00
cot-den-13	0,13	0,31	0,22	0,06	12,00
sch-den-16	0,14	0,51	0,27	0,10	12,00
sch-den-23	0,15	0,52	0,33	0,11	12,00
sch-den-29	0,24	0,67	0,34	0,14	12,00
koy-den-54	0,35	0,75	0,55	0,13	12,00
ple-den-59	0,21	1,74	0,56	0,49	12,00
sch-den-ref1	0,10	0,72	0,34	0,16	20,00
sch-den-ref2	0,12	0,35	0,26	0,09	20,00

4.1.2.8 Nitrate

Very similar to ammonium, the nutrient nitrate is positively correlated to structure ($r = 0.6$, $p < 0.013$), ammonium ($r = 0.7$, $p < 0.001$), water capacity ($r = 0.5$, $p < 0.019$) and phosphate ($r = 0.5$, $p < 0.032$; tab. 19). The highest value was found at **sch-den-23** which had been ash-meliorated for agriculture. Again, **sch-bar-4** shows unexpected high values, indicating a peek in microfloral activity in a soil with low densities of microarthropods. The lowest values were found at the recently meliorated site **cot-spa-4** and the reference site **sch-spa-ref** (fig. 31, tab. 18).

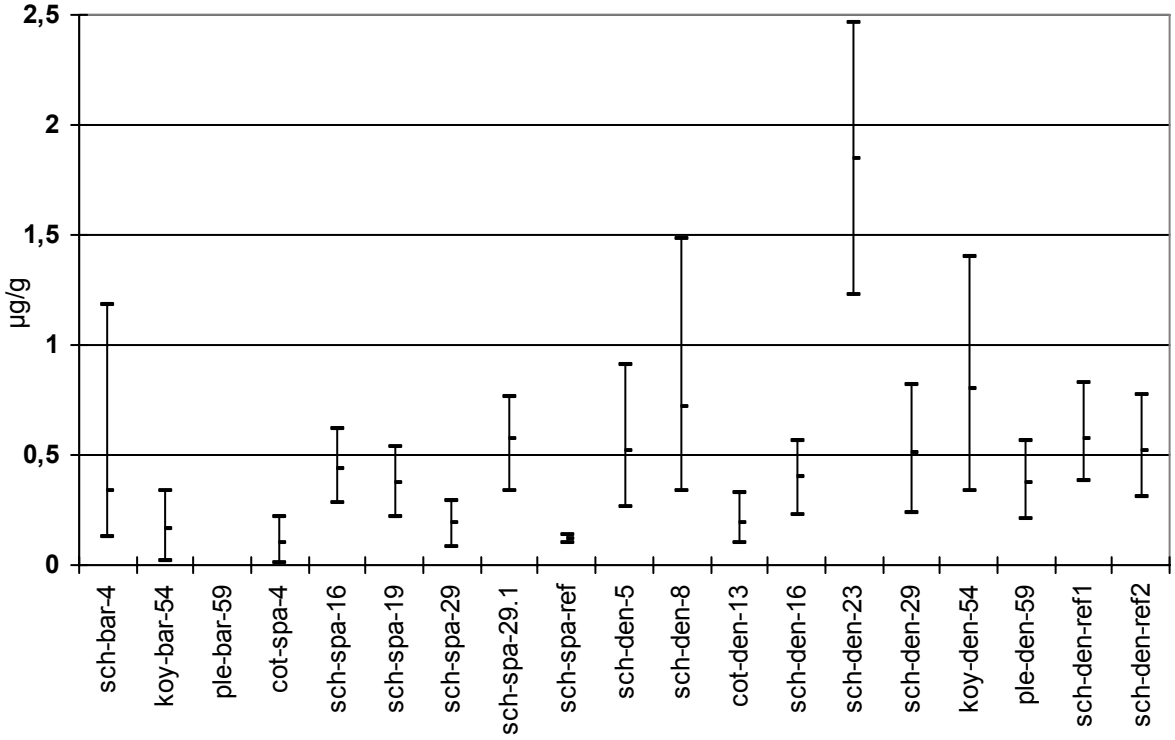


Figure 31: Nitrate (µg/g) in sites of free succession; maximal, minimal and mean values; sites distinguished between vegetation structure and age from left to right: bare substrate, sparse vegetation and dense vegetation.

High deviation was found again at the littoral site **sch-den-8** and the ash-meliorated site **sch-den-23**, but also at the youngest bare site **sch-bar-4**. Least deviation was found at **cot-spa-4**, but it should be kept in mind that only 8 samples could be studied. **Sch-spa-ref** brought only results for 2 samples.

Table 18: Nitrate (µg/g) of sites with free succession, minimal, maximal and mean values, deviation and number of tested samples (n).

	min.	max.	mean	deviation	n
sch-bar-4	0,13	1,18	0,34	0,28	20
koy-bar-54	0,02	0,34	0,16	0,10	10
ple-bar-59	-	-	-	-	0
cot-spa-4	0,01	0,22	0,10	0,10	8
sch-spa-16	0,28	0,62	0,44	0,13	20
sch-spa-19	0,22	0,54	0,37	0,11	20
sch-spa-29	0,08	0,29	0,19	0,09	8
sch-spa-29.1	0,34	0,76	0,57	0,15	12
sch-spa-ref	0,10	0,14	0,12	0,03	2
sch-den-5	0,26	0,91	0,52	0,18	20
sch-den-8	0,34	1,48	0,72	0,40	12
cot-den-13	0,10	0,33	0,19	0,11	6
sch-den-16	0,23	0,56	0,40	0,11	12
sch-den-23	1,23	2,46	1,85	0,39	12

	min.	max.	mean	deviation	n
sch-den-29	0,24	0,82	0,51	0,18	12
koy-den-54	0,34	1,40	0,80	0,38	12
ple-den-59	0,21	0,56	0,37	0,11	12
sch-den-ref1	0,38	0,83	0,57	0,14	20
sch-den-ref2	0,31	0,77	0,52	0,15	20

Table 19: Correlations between soil properties, significant negative correlations blue, significant positive correlations orange (Spearman-Rho).

free succession	pH		Conductivity		Water content		Water capacity		Phosphate		Ammonium		Nitrate		Organic matter content		Structure		Site age
Spearman-Rho	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r
pH	1,0																		
Conductivity	0,7	0,000	1,0																
Water content	0,2	0,458	0,6	0,007	1,0														
Water capacity	0,3	0,210	0,5	0,030	0,6	0,018	1,0												
Phosphate	0,2	0,470	0,3	0,226	0,4	0,073	0,5	0,029	1,0										
Ammonium	0,1	0,553	0,4	0,061	0,6	0,013	0,5	0,017	0,4	0,107	1,0								
Nitrate	0,3	0,232	0,4	0,065	0,4	0,085	0,5	0,019	0,5	0,032	0,7	0,001	1,0						
Organic matter content	0,3	0,226	0,6	0,003	0,8	0,000	0,7	0,002	0,3	0,273	0,7	0,002	0,4	0,080	1,0				
Structure	0,3	0,146	0,4	0,090	0,6	0,011	0,6	0,005	0,6	0,003	0,7	0,000	0,6	0,013	0,7	0,001	1,0		
Site age	-0,2	0,364	-0,3	0,204	0,1	0,652	0,3	0,172	0,2	0,430	0,2	0,407	0,1	0,616	0,3	0,196	0,4	0,067	1,0

4.1.2.9 Cluster analysis

Cluster analysis separates 2 groups containing several subgroups. The 1st group contains the ash-meliorated site **sch-den-23**, which is clearly put separately from the other sites of this group. The remaining 3 subgroups represent the poorest sites, with **koy-bar-54**, **ple-den-59**, **sch-den-ref1** and **sch-den-29** as "richest" of the poor sites, according to organic matter content indicated as loss on ignition. **Koy-bar-54** is probably grouped here because of its high amount of remaining lignite. This group is followed by **sch-bar-4** and **sch-spa-29.1** as sites with intermediate poor soil conditions and as poorest sites **sch-spa-ref**, **sch-spa-19**, **sch-spa-29** (all of them the only sites covered with moss) and **ple-bar-59**.

The 2nd group is also separated into 2 subgroups by its soil richness. The richest soils would be **sch-den-16**, **sch-den-8**, **cot-den-13** and **sch-den-ref2**. The 2nd subgroup contains **koy-den-54, sch-spa-16** and the young meliorated sites **sch-den-5** and **cot-spa-4** (fig. 32).

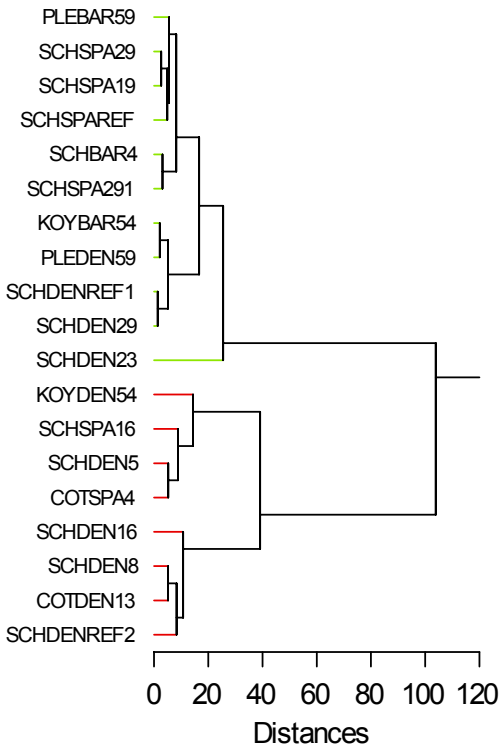


Figure 32: Cluster analysis of studied soil parameters for sites with free succession (Distance metric is Euclidean, Ward minimum variance method).

Table 20: Clustering of sites. Distance metric is Euclidean distance, Ward minimum variance method

Cluster containing	and Cluster containing	were Joined at distance	No. of members in new cluster
SCHDENREF1	SCHDEN29	1.323	2
PLEDEN59	KOYBAR54	2.092	2
SCHSPA29	SCHSPA19	2.646	2
SCHSPA291	SCHBAR4	3.102	2
SCHSPAREF	SCHSPA20	4.852	3
PLEDEN59	SCHSPA29	4.852	3
COTDEN13	SCHDEN8	5.196	2
SCHDEN5	COTSPA4	5.210	2
SCHSPAREF	PLEBAR59	5.519	4
SCHSPAREF	SCHSPA291	8.164	6
COTDEN13	SCHDENREF2	8.281	3
SCHSPA16	SCHDEN5	8.819	3
SCHDEN16	COTDEN13	10.679	4
KOYDEN54	SCHSPA16	14.417	4
SCHSPAREF	PLEDEN59	16.607	10
SCHSPAREF	SCHDEN23	25.468	11
SCHDEN16	KOYDEN54	39.087	8
SCHSPAREF	SCHDEN16	103.858	19

4.1.3 Soil parameters and correlations

Soil parameters were tested for correlations among each other and to **dominance** of collembolan species (SPSS 12.0, Spearman-Rho).

Age:

Significantly positively correlated to age are *Folsomia fimetaria* (r = 0.366, p < 0.047)*, Folsomia penicula* (r = 0.392, p < 0.032)*, Friesea mirabilis* (r = 0.418, p< 0.022)*, Isotomiella minor* (r = 0.417, p < 0.022) and *Lepidocyrtus paradoxus* (r = 0.503, p < 0.028).

Schoetella ununguiculata is **significantly negatively** correlated to age of sites (r = -0.456, p < 0.011).

For *Folsomia candida* (r = 0.331, p < 0.074)*, Protaphorura armata* (r = 0.350, p < 0.058)*, Desoria violacea* (r = 0.352, 0.056), *Lepidocyrtus lignorum* (r = 0.325, p < 0.080) and *Pseudachorutes subcrassus* (r = 0.355, p < 0.055) there is a **tendency** to be found at **older sites.**

Older sites have a **significantly high** organic matter content (r = 0.434, p< 0.017), water capacity (r = 0.423, p < 0.020) and ammonium content (r = 0.382, p < 0.037).

Older sites **tend** to have low pH (r = -0.344, p < 0.063) and more developed structure (r = 0.334, p < 0.071).

Structure:

Significantly positively correlated to structure are *Arrhopalites caecus* (r = 0.435, p < 0.016), *Desoria violacea* (r = 0.376, p < 0.040), *Entomobrya marginata* (r = 0.568, p < 0.001), *E. nivalis* (r = 0.469, p < 0.009), *Folsomia penicula* (r = 0.581, p < 0.001)*, Friesea mirabilis* (r = 0.506, p < 0.004)*, Isotomiella minor* (r = 0.634, 0.000)*, Lepidocyrtus violaceus* (r = 0.402, p < 0.028), *Neanura muscorum* (r = 0.442, p < 0.014), *Orchesella bifasciata* (r = 0.401, p < 0.028), *O. cincta* (r = 0.410, p < 0.024), *O. flavescens* (r = 0.588, p < 0.001), *Protaphorura armata* (r = 0.410, p < 0.024)*, P. meridiata* (r = 0.404, p < 0.027), *Pseudachorutes parvulus* (r = 0.432, p < 0.017), *Vertagopus arboreus* (r = 0.418, p < 0.021), *Willemia anophthalma* (r = 0.577, p < 0.001), *Xenylla acauda* (r = 0.375, p < 0.041) and *Xenylla grisea* (r = 0.416, p < 0.022).

Anurophorus atlanticus (r = 0.352, p < 0.056), *Folsomia candida* (r = 0.326, p < 0.079)*, F. fimetaria* (r = 0.351, p < 0.057)*, Metaphorura affinis* (r = 0.340, p < 0.066), *Micraphorura absoloni* (r = 0.344, p < 0.063) and *Parisotoma notabilis* (r = 0.355, p < 0.054) have a **tendency** to be found at sites with **more developed vegetation**.

Mesaphorura critica has a **tendency** (r = -0.331, p < 0.074) to be found at sites with **weakly developed vegetation.**

Pseudoanurophorus alticolus (r = -0.387, p < 0.035) is **significantly negatively** correlated to structure.

For structural more developed sites there is a **tendency** to have low pH (r = -0.333, p < 0.072) and they tend to be older sites (r = 0.334, p < 0.071).

Structural more developed sites have **significantly higher** organic matter content (r = 0.748, p < 0.000), conductivity (r = 0.438, p < 0.016), water content (r = 0.644, p < 0.000), water capacity (r = 0.733, p < 0.000), ammonium content (r = 0.625, p < 0.000) and nitrate content (r = 0.488, p < 0.008).

pH:

Significantly positively correlated to pH are *Isotomodes productus* (r = 0.482, p < 0.007)*, Isotoma palustris* (r = 0.390, p < 0.033), *Mesaphorura critica* (r = 0.372, p < 0.043) and *Proisotoma minuta* (r = 0.551, p < 0.002).

Mesaphorura krausbaueri (r = 0.358, p < 0.052) and *Ceratophysella succinea* (r = 0.352, p < 0.056) show an almost significant **tendency** to be found at sites with **higher pH**. The tendencies for *Cryptopygus thermophilus* (r = 0.342, p < 0.064) and *Sphaeridia pumilis* (r = 0.332, p < 0.073) are weaker.

A **significantly negative correlation** show *Anurophorus atlanticus* (r = -0.371, p < 0.044), *Desoria violacea* (r = -0.458, p < 0.011), *Entomobrya corticalis* (r = -0.408, p < 0.025), *Isotomiella minor* (r = -0.371, p < 0.044)*, Lepidocyrtus violaceus* (r = -0.408, p < 0.025), *Micraphorura absoloni* (r = -0.476, p < 0.008), *Pseudachorutes parvulus* (r = -0.408, p < 0.025), *Willemia anophthalma* (r = -0.461, p < 0.010) and *Xenylla grisea* (r = -0.432, p < 0.017).

Folsomia penicula (r = -0.354, p < 0.055), *Entomobrya marginalis* (r = -0.331, p < 0.074) and *Metaphorura affinis* show a **tendency** to prefer **acidic sites**.

There is a **tendency** for pH to decrease with time (r = -0.344, p < 0.063) and structure (r = -0.333, p < 0.072).

Organic matter content:

Significantly positively correlated to organic matter content are *Arrhopalites caecus* (r = 0.571, p < 0.001), *Desoria violacea* (r = 0.423, p < 0.020), *Entomobrya corticalis* (r = 0.416, p < 0.022), *Folsomia candida* (r = 0.385, p < 0.035)*, F. fimetaria* (r = 0.405, p < 0.026)*, F. penicula* (r = 0.468, p < 0.009)*, Friesea mirabilis* (r = 0.652, p < 0.000)*, Isotomiella minor* (0.565, p < 0.001)*, Lepidocyrtus violaceus* (r = 0.371, p < 0.044), *Neanura muscorum* (r = 0.425, p < 0.019), *Orchesella bifasciata* (r = 0.391, p < 0.033), *O. flavescens* (r = 0.685, p < 0.000), *Parisotoma notabilis* (r = 0.466, p < 0.009)*, Protaphorura armata* (r = 0.516, p < 0.004), *P. meridiata* (r = 0.373, p < 0.042), *Pseudachorutes parvulus* (r = 0.416, p < 0.022), *Sminthurinus aureus* (r = 0.422, p < 0.020), *Willemia anophthalma* (r = 0.490, p < 0.006) and *Xenylla grisea* (r = 0.400, p < 0.029)*.*

Anurophorus alticolus (r = 0.352, p< 0.057), *Entomobrya nivalis* (r = 0.359, p < 0.051), *Folsomia quadrioculata* (r = 0.328, p < 0.077), *Mesaphorura macrochaeta* (r = 0.334, p < 0.071), *Metaphorura affinis* (r = 0.341, p < 0.066), *Sminthurides schoetti* (r = 0.355, p < 0.054), *Sphaeridia pumilis* (r = 0.332, p < 0.073) show a **tendency** to prefer sites with higher organic matter content.

Mesaphorura atlantica (r = -0.546, p < 0.002), *Pseudoanurophorus alticolus* (r = -0.441, p < 0.015), *Schoetella ununguiculata* (r = -0.445, p < 0.014) have a **significantly negative correlation** to organic matter content.

Organic matter content is **significantly positively** correlated to age (r = 0.434, p < 0.017), structure (r = 748, p < 0.000), conductivity (r = 0.714, p < 0.000), water content (r = 0.885, p < 0.000), water capacity (r = 0.833, p < 0.000), ammonium (r = 0.742, p < 0.000) and nitrate (r = 0.485, p < 0.009).

Conductivity:

Significantly positively correlated to conductivity are *Arrhopalites caecus* (r = 0.497, p < 0.005), *Friesea mirabilis* (r = 0.374, p < 0.042), *Isotomodes productus* (r = 0.465, p < 0.010), *Neanura muscorum* (r = 0.413, p < 0.023), *Orchesella flavescens* (r = 0.553, p < 0.002), *Parisotoma notabilis* (r = 0.546, p < 0.002), *Sminthurides schoetti* (r = 0.449, p < 0.013), *Sminthurinus aureus* (r = 0.514, p < 0.004) and *Sphaeridia pumilis* (r = 0.461, p < 0.010).

Pseudosinella alba (r = 0.356, p < 0.054) and *Lepidocyrtus violaceus* (0.338, p < 0.068) show a **tendency** to prefer sites with **higher conductivity**.

Mesaphorura atlantica (r = -0.533, p < 0.002), *Pseudoanurophorus alticolus* (r = -0.511, p < 0.004) and *Sminthurus nigromaculatus* (r = -0.372, p < 0.043) have a **significantly negative** correlation to conductivity.

Micranurida musci (r = -0.326, p < 0.079) shows a **tendency** to prefer poor sites with **low conductivity.**

Conductivity is **significantly positively** correlated to structure (r = 0.438, p < 0.016), organic matter content (r = 0.737, p < 0.000), water capacity (r = 0.644, p < 0.000), water content (r = 0.737, p < 0.000), ammonium (r = 0.578, p < 0.001) and nitrate (r = 0.597, p < 0.001).

Water content:

Significantly positively correlated to water content are *Arrhopalites caecus* (r = 0.443, p < 0.016), *Desoria violacea* (r = 0.450, p < 0.014), *Entomobrya corticalis* (r = 0.406, p < 0.029), *Entomobrya nivalis* (r = 0.391, p < 0.036), *Folsomia candida* (r = 0.447, p < 0.015)*, F. penicula* (r = 0.415, p < 0.025)*, Friesea mirabilis* (r = 0.427, p < 0.021)*, Isotomiella minor* (r = 0.450, p < 0.014)*, Neanura muscorum* (r = 0.443, p < 0.016), *Orchesella flavescens* (r = 0.706, p < 0.000), *Parisotoma notabilis* (r = 0.445, p < 0.015), *Pseudachorutes parvulus* (r = 0.406, p < 0.029), *Sminthurinus aureus* (r =

0.465, p < 0.011), *Sphaeridia pumilis* (r = 0.461, p < 0.012) and *Willemia anophthalma* (r = 0.588, p < 0.001).

Folsomia fimetaria (r = 0.356, p < 0.058), *Lepidocyrtus violaceus* (r = 0.343, p < 0.068), *Mesaphorura macrochaeta* (r = 0.333, p < 0.078), *Micraphorura absoloni* (r = 0.343, p < 0.016), *Protaphorura armata* (r = 0.364, p < 0.052) and *Xenylla grisea* (r = 0.355, p < 0.059) have a **tendency** to be found at moist sites.

Mesaphorura atlantica (r = -0.542, p < 0.002) and *Schoetella ununguiculata* (r = -0.446, p < 0.015) have a **significantly negative** correlation to water content.

Water content is **significantly correlated** to structure (r = 0.644, p < 0.000), organic matter content (r = 0.885, p < 0.000), conductivity (r = 0.737, p < 0.000), water capacity (r = 0.781, p < 0.000), ammonium (r = 0.739, p < 0.000) and nitrate (r = 0.523, p < 0.005).

Water capacity:

Significantly positively correlated to water capacity are *Desoria violacea* (r = 0.458, p < 0.011), *Entomobrya corticalis* (r = 0.416, p < 0.022), *Entomobrya nivalis* (r = 0.420, p < 0.021), *Folsomia candida* (r = 0.453, p < 0.012)*, F. penicula* (r = 0.493, p < 0.006), *Friesea mirabilis* (r = 0.557, p < 0.001)*, Isotomiella minor* (r = 0.625, p < 0.000)*, Lepidocyrtus violaceus* (r = 0.371, p < 0.044), *Micraphorura absoloni* (r = 0.381, p < 0.038), *Metaphorura affinis* (r = 0.368, p < 0.046)*, Neanura muscorum* (r = 0.381, p < 0.038), *Orchesella bifasciata* (r = 0.419, p < 0.021), *O. flavescens* (r = 0.703, p < 0.000), *Parisotoma notabilis* (r = 0.378, p < 0.039)*, Protaphorura armata* (r = 0.462, 0.010), *P. meridiata* (r = 0.378, p < 0.039), *Pseudachorutes parvulus* (r = 0.416, p < 0.022) and *Willemia anophthalma* (r = 0.572, p < 0.001) and *Xenylla grisea* (r = 0.400, p < 0.029).

Arrhopalites caecus (r = 0.346, p < 0.061), *Orchesella cincta* (r = 0.328, p < 0.077) and *Sminthurinus aureus* (r = 0.351, p < 0.057) have a **tendency** to be found at sites with higher water capacity.

Mesaphorura atlantica (r = -0.441, p < 0.015), *Pseudoanurophorus alticolus* (r = -0.403, p < 0.027) and *Schoetella ununguiculata* (r = -0.482, p < 0.007) have a **significantly negative** correlation to water capacity.

Water capacity is **significantly correlated** to age (r = 0.423, p < 0.020), structure (r = 0.733, p < 0.000), organic matter content (r = 0.833, p < 0.000), conductivity (r = 0.644, p < 0.000), water content (r = 0.781, p < 0.000), ammonium (r = 0.705, p < 0.000) and nitrate (r = 0.595, p < 0.000).

Phosphate:

Significantly positively correlated to phosphate are *Folsomia candida* (r = 0.487, p < 0.006)*, Isotomodes productus* (r = 0.376, p < 0.041), *Parisotoma notabilis* (r = 0.482, p < 0.007) and *Sphaeridia pumilis* (r = 0.456, p < 0.011).

Cyphoderus albinus (r = 0.352, p < 0.057)*, Ceratophysella succinea* (r = 0.325, p < 0.080) and *Seira domestica* (r = 0.326, p < 0.079) have a **tendency** to prefer sites which are richer in phosphate.

Brachystomella parvula (r = -0.353, p < 0.056) has a **tendency not** to be found at sites richer in phosphate.

Ammonium:

Significantly positively correlated to ammonium are *Arrhopalites caecus* (r = 0.366, p < 0.041), *Cyphoderus albinus* (r = 0.371, p < 0.044)*, Desoria violacea* (r = 0.509, p < 0.004), *Entomobrya corticalis* (r = 0.433, p < 0.017), *Entomobrya nivalis* (r = 0.392, p < 0.032), *Folsomia candida* (r = 0.577, p < 0.001)*, F. fimetaria* (r = 0.416, p < 0.022), *Folsomia penicula* (r = 0.486, p < 0.006)*, Friesea mirabilis* (r = 0.437, p < 0.016)*, Isotomiella minor* (r = 0.411, p < 0.024)*, Lepidocyrtus lanuginosus* (r = 0.455, p < 0.014), *Metaphorura affinis* (r = 0.430, p < 0.018)*, Neanura muscorum* (r = 0.521, p < 0.003), *Orchesella flavescens* (r = 0.563, p < 0.001), *Parisotoma notabilis* (r = 0.593, p < 0.001)*, Protaphorura armata* (r = 0.487, p < 0.006)*, P. meridiata* (r = 0.407, p < 0.026), *Pseudachorutes parvulus* (r = 0.433, p < 0.017), *P. subcrassus* (r = 0.401, p < 0.028), *Sphaeridia pumilis* (r = 0.390, p < 0.033) and *Willemia anophthalma* (r = 0.575, p < 0.001).

Mesaphorura atlantica (r = -0.545, p < 0.002) *Pseudoanurophorus alticolus* (r = -0.418, p < 0.022) and *Schoetella ununguiculata* (r = -0.415, p < 0.023) have a **significantly negative** correlation to ammonium.

Anurophorus atlanticus (r = 0.353, p < 0.056), *Folsomia quadrioculata* (r = 0.325, p < 0.079), *Lepidocyrtus violaceus* (r = 0.343, p < 0.063) and *Orchesella bifasciata* (r = 0.356, p < 0.054) have a **tendency** to be found at sites with low ammonium.

Ammonium is **significantly correlated** to age (r = 0.382, p < 0.037), structure (r = 0.625, p < 0.000), organic matter content (r = 0.742, p < 0.000), conductivity (r = 0.578, p < 0.001), water content (r = 0.739, p < 0.000), water capacity (r = 0.705, p < 0.000) and nitrate (r = 0.598, p < 0.001).

Nitrate:

Significantly positively correlated to nitrate are *Desoria violacea* (r = 0.377, p < 0.048), *Lepidocyrtus cyaneus* (r = 0.388, p < 0.041), *Orchesella flavescens* (r =

0.554, p < 0.002), *Parisotoma notabilis* (r = 0.459, p < 0.014), *Sminthurides schoetti* (r = 0.482, p < 0.009) and *Sphaeridia pumilis* (r = 0.405, p < 0.033).

Entomobrya marginata (r = 0.357, p < 0.063), *Friesea mirabilis* (r = 0.352, p < 0.066), *Isotomiella minor* (r = 0.349, p < 0.069) and *Lepidocyrtus violaceus* (r = 0.359, p < 0.060) show a **tendency** to be found at sites with **high nitrate** content.

Pseudoanurophorus alticolus (r = -0.344, p < 0.073) has a **tendency** to be found at sites with **low nitrate** content.

Nitrate is **significantly correlated** to structure (r = 0.488, p < 0.008), organic matter content (r = 0.485, p < 0.009), conductivity (r = 0.597, p < 0.001), water content (r = 0.523, p < 0.005), water capacity (r = 0.595, p < 0.001) and ammonium (r = 0.598, p < 0.001).

4.2 Collembola

At all study sites, 13.733 specimens, distributed across 84 species were identified. No species was eudominant, and only 2 species (*Mesaphorura macrochaeta, Parisotoma notabilis*) dominant. 3 species were subdominant (*Isotomiella minor, Folsomia penicula, Isotoma anglicana*). 15 species were recedent, so the large number of 69 species was subrecedent (Figure 33). The juveniles of *Mesaphorura spec.* are also recorded in this table as they represent quite a large amount of specimen. They are most probable mainly juveniles of *Mesaphorura macrochaeta*.

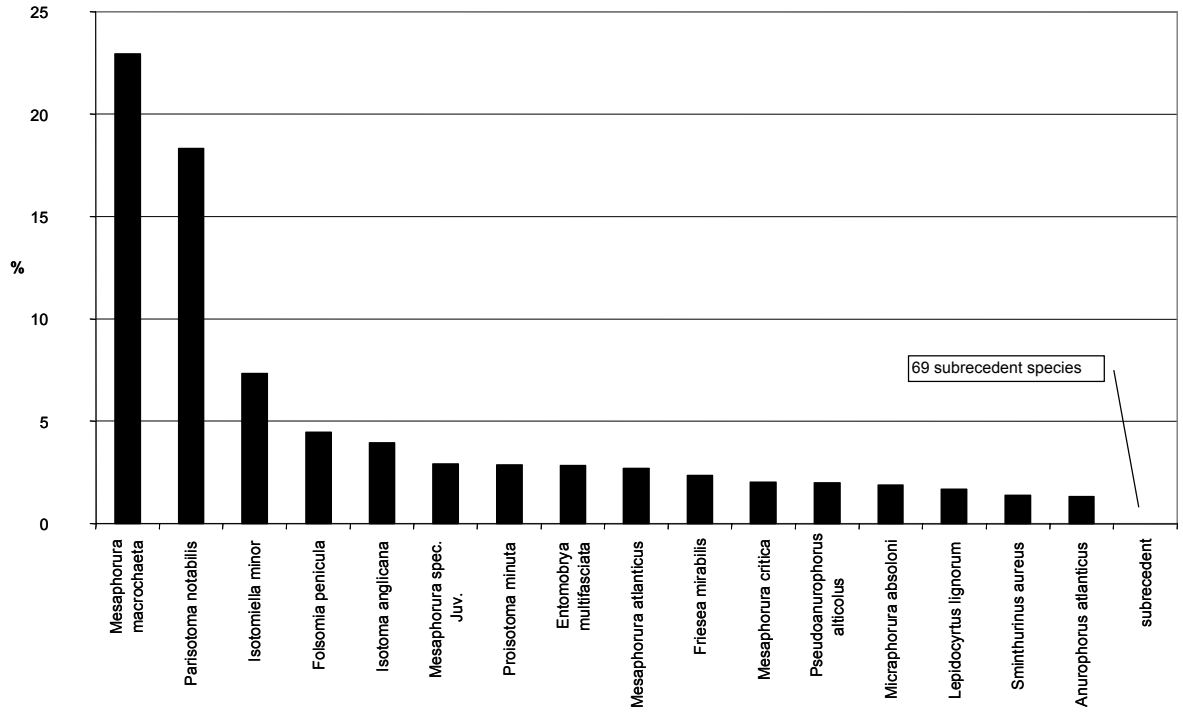


Figure 33: Dominance scale for all study sites.

4.2.1 Afforested sites

4.2.1.1 Species composition and dominance scale

6.119 specimens, distributed across 67 species were identified.

Species number is between 14 and 17 at the younger sites of the chronosequence. An exception with 23 species is **ple-pin-20**, where stand age is comparable to the other younger sites, but site age is much older (approximately > 50 years). At the slightly older sites at Koyne, number of species is with 20 and 19 species slightly higher than at the younger sites (**koy-oak-24**, **koy-oak-34**). The highest number of species was found at the oldest reclamation site at Plessa (≈ 43 years) with a species number equal to that of the 44-years-old reference site **alt-oak-44**. Both stands are of about the same age and afforested with *Quercus rubra*. The youngest reference site

has a higher species richness than all reclamation sites but the oldest one. Species number reaches its climax at the oldest reference site (38 species). After 43 years, species number in the reclamation site equals that of the reference site (fig. 34).

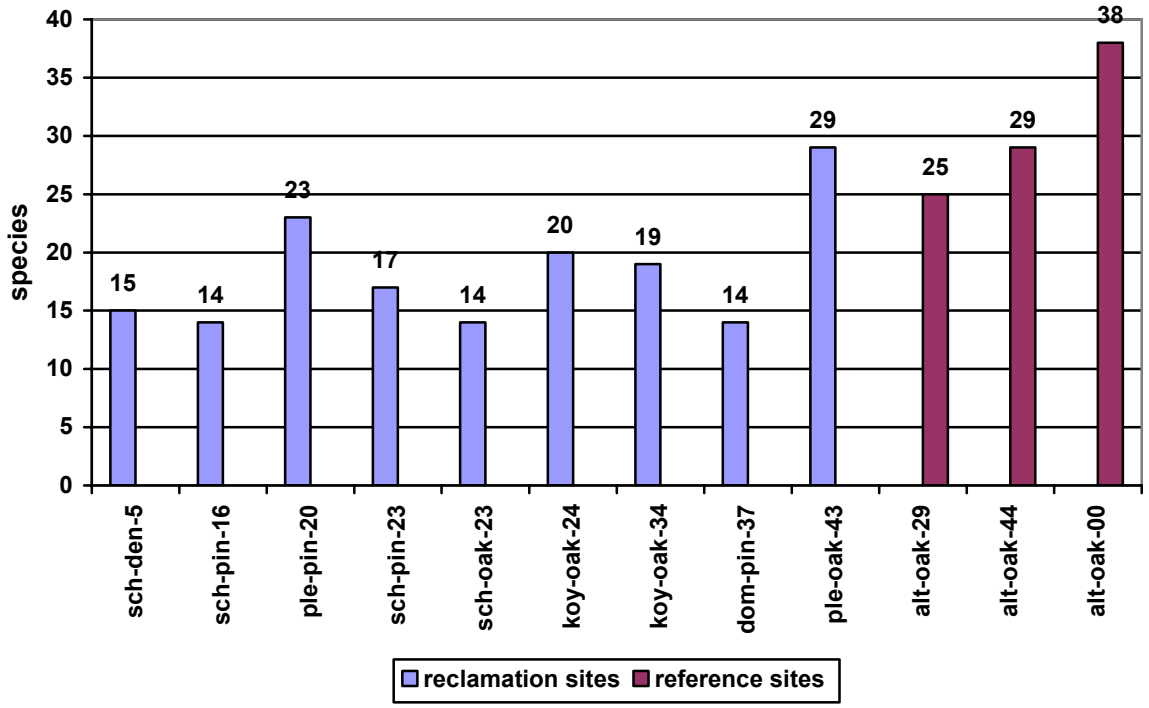


Figure 34: Number of species in afforested sites.

If the reference sites are included, Spearman-Rho shows a significant high correlation between stand age and increase of species ($r = 0.65$, $p < 0.022$). However, if the reference sites are not included, then there is no significant correlation between stand age and increase of species ($r = 0.332$, $p < 0.383$).

Specimens per sampling: At the youngest reclamation site **sch-den-5** with its dense vegetation cover, number of specimens per sampling is about as high as at the older reclamation sites and the youngest reference site. But there is a strong decrease (48 to 19 specimens) from **sch-den-5** to **sch-pin-16,** which has no herb layer at all. Abundance increases and varies between 50 specimens at **sch-pin-23** and 115 specimens at **koy-oak-34**. The youngest reference site **alt-oak-29** shows fewer specimens per sampling (41) than the reclamation sites with the exception of **sch-pin-16** (19). In the older reference sites, number of specimens is 2 to 5 times higher than at the oldest reclamation site (fig. 35).

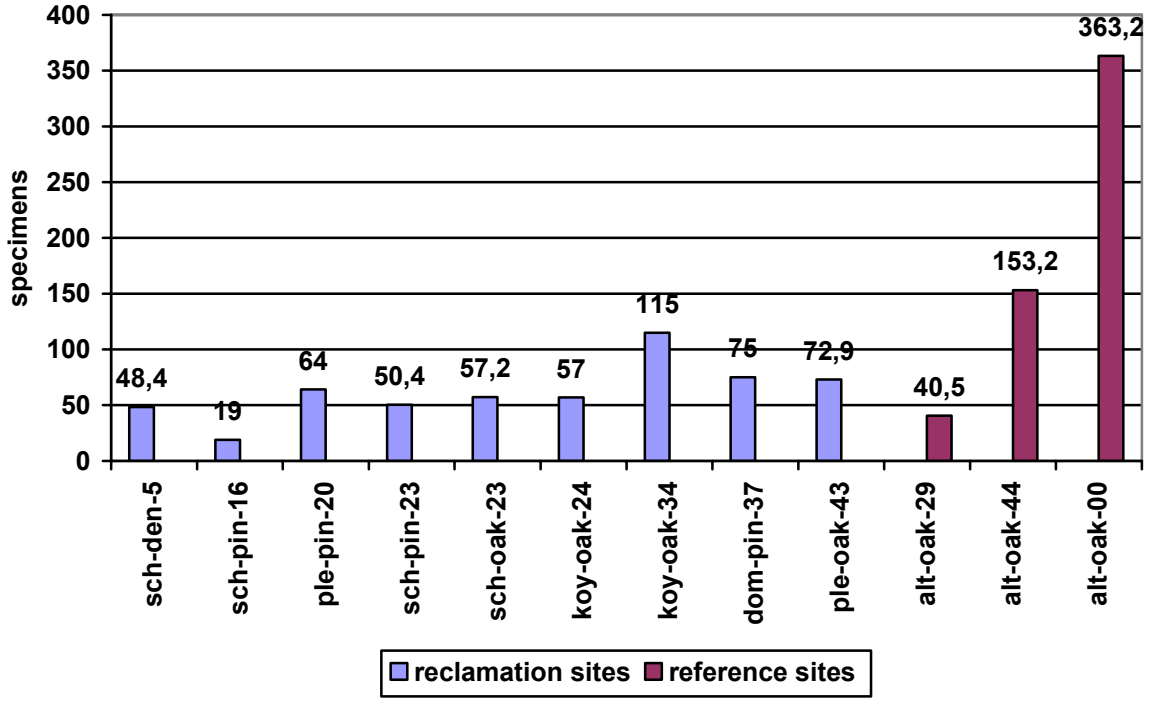


Figure 35: Number of specimens per sampling in afforested sites.

Spearman-Rho shows that the increase of specimens with time is significantly high ($r = 0.616$, $p < 0.033$) if the reference sites are included. But similar to the increase of species, there is no significant increase in number of specimens per sampling, if the reference sites are excluded ($r = 0.636$, $p < 0.066$).

For the restoration of a forest-ecosystem on reclaimed land, these data would suggest, that it takes at least 40 years for a comparable number of species to establish. But 40 years are not sufficient to establish an abundance which is comparable to that of the reference sites. Therefore, the following results concerning the ecological groups will be looked at on the species level and on the level of specimens per sampling.

Dominance scale of all afforested sites

No species is eudominant. There are 2 dominant species: *Mesaphorura macrochaeta* (25.9 %) and *Isotomiella minor* (15.0 %). 4 species are subdominant: *Parisotoma notabilis* (11.6 %), *Folsomia penicula* (9.4 %), *Friesea mirabilis* (4.6 %) and *Micraphorura absoloni* (4.0%). The other 58 species are recedent (8 species) and subrecedent (50 species).

Distinguished between reclamation sites and reference sites, dominance scales look different. At the reclamation sites, *Mesaphorura macrochaeta* is eudominant (Mes mac, 41.5 %), followed by *Parisotoma notabilis* as single dominant species (Par not, 19.2 %). Both species are more typical for open habitats. *Isotoma anglicana* (Iso ang, 4.3 %) is the only subdominant species (fig. 36). All other species are recedent (10 species) and subrecedent (35 species).

At the reference sites, there is no eudominant species. The forest species *Isotomiella minor* (Iso min, 29.2 %) and *Folsomia penicula* (Fol pen, 18.0 %) are the dominant species. 4 more species are subdominant: *Mesaphorura macrochaeta* (Mes mac, 10.4 %), *Micraphorura absoloni* (Mic abs, 8.1 %), *Friesea mirabilis* (Fri mir, 6.6 %) and *Anurophorus atlanticus* (Anu atl, 5.7 %; fig. 36). *Parisotoma notabilis* (Par not, 3.9 %) and 2 more species are recedent, 41 species are subrecedent.

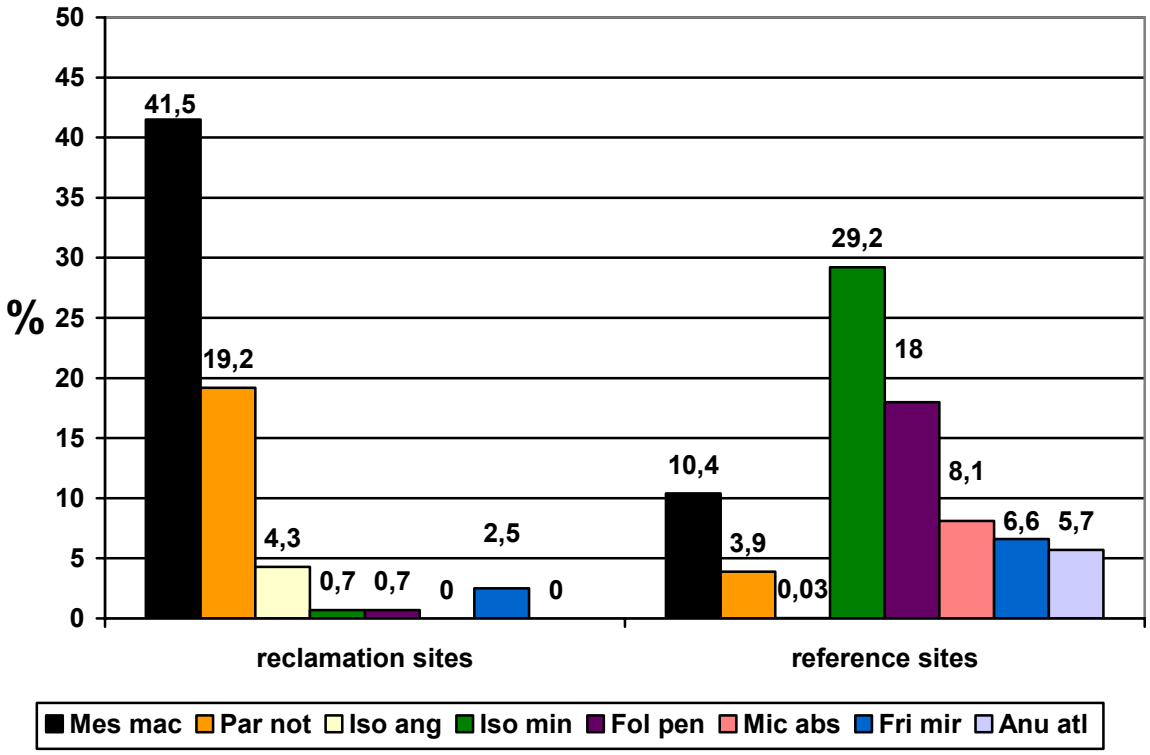


Figure 36: Dominances of Collembola at 9 reclamation sites and 3 reference sites (dominant and subdominant species only).

17 species are missing in the reclamation sites: *Anurophorus atlanticus, Arrhopalites caecus, Bourletiella pruinosa, Ceratophysella denticulata, Entomobrya corticalis, Lepidocyrtus violaceus, Megalothorax minimus, Mesaphorura yosii, Metaphorura affinis, Micraphorura absoloni, Pseudachorutes parvulus, P. subcrassus, Pseudosinella alba, Sminthurides schoetti, Tomocerus minor, Xenylla brevicauda, X. grisea*.

14 species are missing in the reference sites: *Ceratophysella succinea, Cryptopygus thermophilus, Entomobrya marginata, E. muscorum, Gisinianus flammeolus, Isotoma viridis, Lepidocyrtus curvicollis, Mesaphorura tenuisensillata, Orchesella villosa, Paratullbergia macdougalli, Pseudoanurophorus alticolus, Schoetella ununguiculata, Tomocerus vulgaris, Willemia aspinata.*

4.2.1.2 Succession of ecological groups

Species, absolute numbers

Syvicolous species increase with time. Species number almost doubles every decade until after 40 years it is comparable to young afforestations on undisturbed soil. After 24 years, there are for the first time more forest species than species of open habitats. Their number increases from 1 at the youngest site **sch-den-5** to 22 at the oldest reference site **alt-oak-00** (fig. 37, tab. 21). Spearman-Rho shows a significantly high positive correlation between stand age and number of sylvicolous species ($r = 0.849$, $p < 0.000$). There is also a significant correlation to ammonium, water content and water capacity and organic matter content. pH is significantly negatively correlated (tab. 22). The increase is still significant, if the reference sites are excluded ($r = 0.856$, $p < 0.003$). However, now there is a significant negative correlation to meadow species and only for ammonium, water capacity and organic matter content there is still a significant positive correlation.

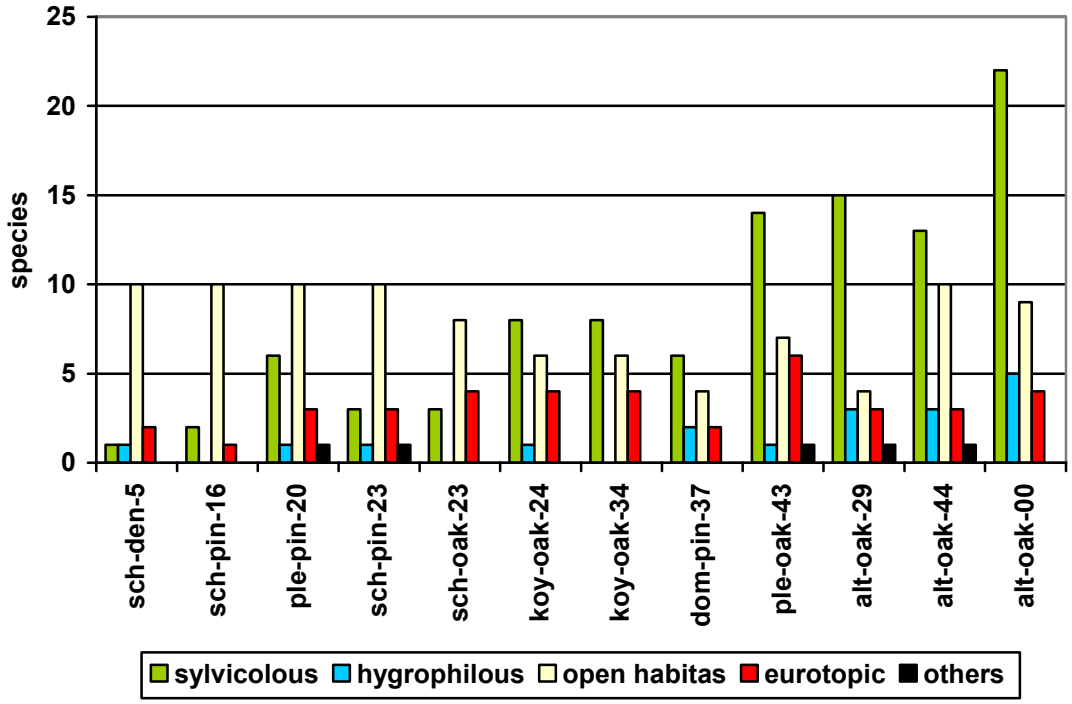


Figure 37: Ecological groups (number of species).

Number of meadow species stays the same for about 20 years (10 species). Afterwards, it declines slightly in stands of about 25 to 40 years of age to a minimum of 4 species at **dom-pin-73** and **alt-oak-29** each. At the oldest reference sites **alt-oak-44** and **alt-oak-00** it increases again after to 10 and 9 species (fig. 37). If one was to use a linear diagram, the line representing meadow species would be trough-like or inverted Ω-shaped. Before canopy closure at a stand age of about 23 years, number of these species stays constant. With canopy closure, their number declines and only in the older sites where canopy is again heterogeneous their number increases again. There is no correlation to stand age ($r = 0{,}509$, $p < 0.91$) or any

other significant correlations. But there already is an almost significant negative correlation to water capacity and organic matter content (tab. 22). But if the reference sites are excluded, than there are some highly significant negative correlations to stand age, ammonium, water content, water capacity and organic matter content (tab. 23). These different results reflect the invertedt Ω-shape of species development.

Number of hygrophilous species varies between 0 and 2 on reclamation sites. In the reference sites, their number is two times higher (3 to 5; fig. 37, tab. 21). There is a significant positive correlation to age of sites ($r = 0.609$, $p < 0.036$) if the reference sites are included. There is also a significant correlation to ammonium, nitrate, water content and water capacity, organic matter content and conductivity (tab. 22). If the reference sites are not included than there are no significant correlations (tab. 23).

Eurotopic species increase slightly from 2 species in the youngest site **sch-den-5** to 4 species in the oldest reference site **alt-oak-00**. There is a single peek of 6 species in the oldest reclamation site **ple-oak-43** (fig. 37, tab. 21). There is no correlation between number of eurotopic species and stand age ($r = 0.076$, $p < 0.814$) or any other correlations (tab. 22). If the reference sites are excluded, there is still no significant correlation, but a tendency for eurotopic species to be found in older stands on reclamation sites (tab. 23).

There are 0 to 1 other species which could not be classified as explained above (fig. 37). They are not correlated significantly to any tested parameter no matter if the reference sites are included (tab. 22) or not (tab. 23).

Table 21: Ecological groups (number of species).

	sch-den-5	sch-pin-16	ple-pin-20	sch-pin-23	sch-oak-23	koy-oak-24	koy-oak-34	dom-pin-37	ple-oak-43	alt-oak-29	alt-oak-44	alt-oak-00
sylvicolous	1	2	6	3	3	8	8	6	14	15	13	22
hygrophilous	1	0	1	1	0	1	0	2	1	3	3	5
open habitats	10	10	10	10	8	6	6	4	7	4	10	9
eurotopic	2	1	3	3	4	4	4	2	6	3	3	4
others	0	0	1	1	0	0	0	0	1	1	1	0
total	14	13	21	18	15	19	18	14	29	26	30	40

Table 22: Correlations of ecological groups (species level) and soil parameters, reference sites are included. Significant positive correlations are marked bright orange, significant negative correlations are marked bright blue.

Altsorgefeld included	forest		hygro		meadow		eurotopic		others	
	r	p	r	p	r	p	r	p	r	p
forest	1,000	0,000								
hygro	0,644	0,024	1,000	0,000						
meadow	-0,474	0,120	-0,143	0,658	1,000	0,000				
eurotopic	0,588	0,044	-0,038	0,907	-0,340	0,279	1,000	0,000		
others	0,320	0,311	0,333	0,290	0,204	0,525	0,076	0,814	1,000	0,000
stand age	0,849	0,000	0,609	0,036	-0,423	0,171	0,509	0,091	0,147	0,648
ammonium	0,787	0,002	0,600	0,039	-0,353	0,260	0,436	0,157	0,122	0,705
phosphate	-0,410	0,185	-0,423	0,170	-0,104	0,748	-0,065	0,840	-0,245	0,442
nitrate	0,474	0,141	0,682	0,021	-0,419	0,199	-0,073	0,831	0,389	0,237
pH	-0,656	0,021	-0,501	0,097	0,259	0,416	-0,284	0,370	-0,172	0,593
water content	0,622	0,041	0,640	0,034	-0,500	0,117	0,091	0,791	-0,173	0,611
water capacity	0,798	0,002	0,728	0,007	-0,546	0,066	0,320	0,311	0,073	0,821
organic matter	0,787	0,002	0,699	0,011	-0,546	0,066	0,367	0,241	0,073	0,821
conductivity	0,562	0,057	0,714	0,009	-0,506	0,093	0,000	1,000	0,171	0,594

Table 23: Correlations of ecological groups (species level) and soil parameters, reference sites are excluded. Significant positive correlations are marked bright orange, significant negative correlations are marked bright blue.

Altsorgefeld excluded	forest		hygro		meadow		eurotopic		others	
	r	p	r	p	r	p	r	p	r	p
forest	1,000	0,000								
hygro	0,179	0,644	1,000	0,000						
meadow	-0,682	0,043	-0,235	0,543	1,000	0,000				
eurotopic	0,016	0,766	-0,143	0,713	-0,408	0,275	1,000	0,000		
others	0,277	0,470	0,306	0,423	0,383	0,309	0,281	0,464	1,000	0,000
stand age	0,856	0,003	0,281	0,464	-0,830	0,006	0,631	0,068	0,138	0,724
ammonium	0,684	0,020	0,261	0,498	-0,761	0,017	0,530	0,142	-0,091	0,815
phosphate	-0,169	0,664	0,056	0,886	-0,017	0,964	0,060	0,878	-0,183	0,638
nitrate	0,358	0,384	0,505	0,202	-0,525	0,182	0,136	0,748	0,190	0,652
pH	-0,314	0,411	0,253	0,512	0,329	0,387	-0,343	0,366	0,046	0,907
water content	0,582	0,130	0,365	0,374	-0,884	0,004	0,282	0,498	-0,282	0,499
water capacity	0,751	0,020	0,373	0,323	-0,883	0,002	0,487	0,183	0,000	1,000
organic matter	0,709	0,032	0,298	0,436	-0,857	0,003	0,564	0,113	0,000	1,000
conductivity	0,346	0,362	0,447	0,227	-0,603	0,085	0,154	0,693	0,000	1,000

Dominance of ecological groups (species level)

To interpret the changing roles of the ecological groups, the dominances on species level were calculated for each site (fig. 38, tab. 24).

The increase of sylvicolous species is highly significantly correlated to stand age ($r = 0.837$, $p < 0.001$). Positive correlation is even higher if the reference sites are excluded ($r = 0.929$, $p < 0.000$). Their dominance increases from 7.1 % at **sch-den-5** to 55.0 % at the oldest reference site **alt-oak-00**. Its highest value is reached at **alt-oak-29** with 57.7 % with its closed canopy (fig. 38, tab. 24).

The decline in dominance of meadow species is significantly high negatively correlated to stand age ($r = -0.786$, $p < 0.002$). With the reference sites excluded, the significance is even higher ($r = -0.912$, $p < 0.001$). Their dominance declines from 71.4 % at **sch-den-5** and 76.9 % at **sch-pin-16** to 22.5 % at the oldest reference site **alt-oak-00** with a minimum of 15.4 % at **alt-oak-29** (fig. 38, tab. 24).

There is a weak positive correlation between the dominance of hygrophilous species and stand age which is not significant ($r = 0.434$, $p < 0.159$), but if the reference sites are excluded, there is no correlation at all ($r = 0.009$, $p < 0.983$). At the reclamation sites, their dominance varies between 4.8 % and 14.3 %. At 3 sites, no hygrophilous species were found. At all 3 reference sites, their dominance is between 10 % and 12.5 %.

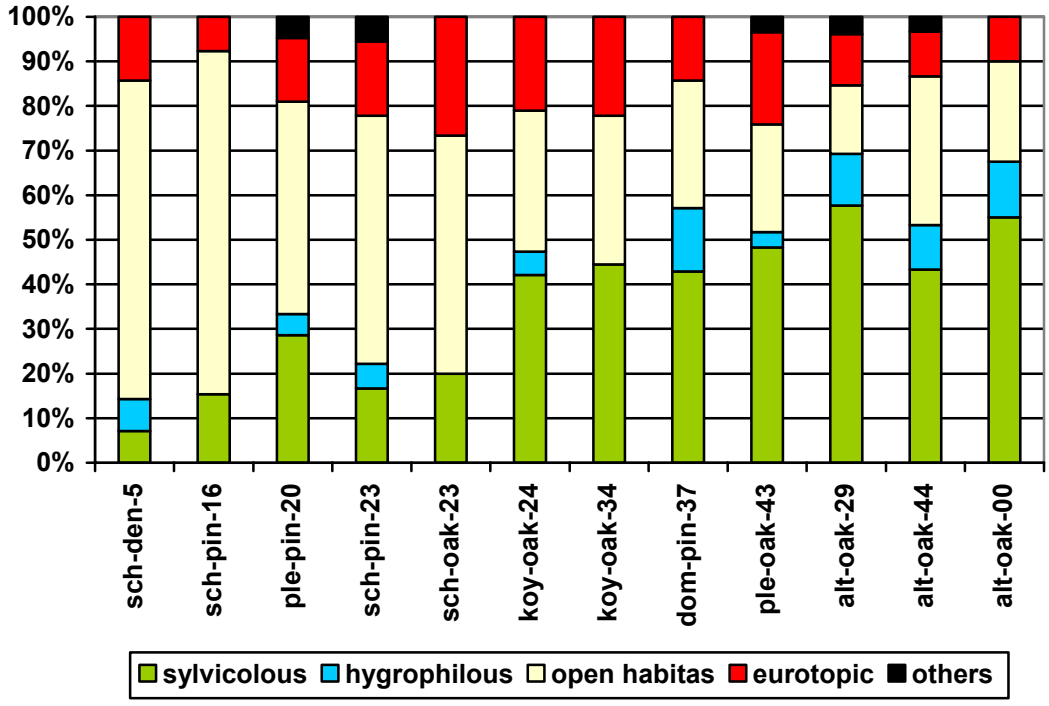


Figure 38: Dominance of ecological groups, species level.

For eurotopic species, there is no correlation to stand age ($r = -0.091$, $p < 0.768$). If the reference sites are excluded, there is a non-significant positive correlation to stand age ($r = 0.477$, $p < 0.195$). With values of about 21 % to 27 % (except **dom-pin-37**: 14.3 %), eurotopic species reach their highest dominances in stands which are about 25 to 43 years old, but only on reclaimed land. At the younger sites, their

dominance is about 15 % with the exception of **sch-pin-16**, where it is only 7.7 %. At the 3 reference sites, their dominance with 10.0 % to 11.5 % is almost constant and lower than in all but one reclamation sites.

Not classified species vary from 0 to 6.7 % of all species (fig. 38, tab. 24).

For about the first 23 years, meadow species are the eudominant ecological group at the reclamation sites. After that, there is a change, for forest species become the eudominant group (Table 24). As ecosystems can be defined by their eudominant ecological groups (CHERNOVA & KUZNETSOVA 2000), there is a change from open habitat to forest on reclamation sites after about 23 years, if one looks at the species level.

Table 24: Dominance of ecological groups, species level. Eudominant groups are marked red.

	sch-den-5	sch-pin-16	ple-pin-20	sch-pin-23	sch-oak-23	koy-oak-24	koy-oak-34	dom-pin-37	ple-oak-43	alt-oak-29	alt-oak-44	alt-oak-00
sylvicolous	7,1	15,4	28,6	16,7	20,0	42,1	44,4	42,9	48,3	57,7	43,3	55,0
hygrophilous	7,1	0,0	4,8	5,6	0,0	5,3	0,0	14,3	3,4	11,5	10,0	12,5
open habitats	71,4	76,9	47,6	55,6	53,3	31,6	33,3	28,6	24,1	15,4	33,3	22,5
eurotopic	14,3	7,7	14,3	16,7	26,7	21,1	22,2	14,3	20,7	11,5	10,0	10,0
others	0,0	0,0	4,8	5,6	0,0	0,0	0,0	0,0	3,4	3,8	3,3	0,0

Table 25: Correlations of changing dominances of ecological groups (species level) and soil parameters, reference sites are included. Significant positive correlations are marked bright orange, significant negative correlations are marked bright blue.

Altsorgefeld included	forest		hygro		meadow		eurotopic		others	
	r	p	r	p	r	p	r	p	r	p
forest	1,000	0,000								
hygro	0,352	0,262	1,000	0,000						
meadow	-0,935	0,000	-0,519	0,084	1,000	0,000				
eurotopic	-0,074	0,819	-0,476	0,118	0,034	0,918	1,000	0,000		
others	0,140	0,663	0,094	0,771	-0,094	0,772	-0,079	0,808	1,000	0,000
stand age	0,873	0,001	0,434	0,159	-0,786	0,002	-0,095	0,768	-0,016	0,962
ammonium	0,738	0,003	0,451	0,141	-0,694	0,012	-0,095	0,768	-0,062	0,847
phosphate	-0,273	0,390	-0,307	0,332	0,216	0,501	0,345	0,273	-0,289	0,362
nitrate	0,469	0,145	0,708	0,015	-0,568	0,068	-0,183	0,590	0,396	0,228
pH	-0,628	0,029	-0,360	0,250	0,513	0,088	0,150	0,641	-0,153	0,636
water content	0,691	0,019	0,670	0,024	-0,679	0,022	-0,169	0,619	-0,312	0,350
water capacity	0,825	0,001	0,655	0,021	0,827	0,001	-0,141	0,662	-0,039	0,904
organic matter	0,825	0,001	0,606	0,037	-0,830	0,001	-0,113	0,727	-0,062	0,847
conductivity	0,629	0,028	0,754	0,005	-0,655	0,021	-0,215	0,502	0,094	0,772

Table 26: Correlations of changing dominances of ecological groups (species level) and soil parameters, reference sites are excluded. Significant positive correlations are marked bright orange, significant negative correlations are marked bright blue.

Altsorgefeld excluded	forest		hygro		meadow		eurotopic		others	
	r	p	r	p	r	p	r	p	r	p
forest	1,000	0,000								
hygro	-0,136	0,728	1,000	0,000						
meadow	-0,933	0,000	-0,153	0,695	1,000	0,000				
eurotopic	O,458	0,215	-0,379	0,314	-0,390	0,300	1,000	0,000		
others	0,059	0,879	0,151	0,698	-0,059	0,879	-0,111	0,777	1,000	0,000
stand age	0,929	0,000	0,009	0,983	-0,912	0,001	0,477	0,195	0,045	0,909
ammonium	0,750	0,020	0,170	0,663	-0,733	0,025	0,458	0,215	-0,168	0,665
phosphate	-0,017	0,966	0,051	0,897	-0,083	0,831	0,051	0,897	-0,297	0,438
nitrate	0,347	0,399	0,393	0,336	-0,491	0,217	0,205	0,627	0,243	0,562
pH	-0,268	0,486	0,204	0,598	0,126	0,748	-0,596	0,090	-0,075	0,849
water content	0,738	0,037	0,317	0,444	-0,714	0,047	0,275	0,509	-0,327	0,429
water capacity	0,850	0,004	0,203	0,600	-0,850	0,004	0,458	0,215	-0,040	0,919
organic matter	0,850	0,004	0,085	0,828	-0,867	0,002	0,525	0,146	-0,079	0,893
conductivity	0,450	0,224	0,458	0,215	-0,483	0,187	0,220	0,569	0,040	0,919

Specimens per sampling

As for technical reasons some sites were sampled less often than others, abundance is given as the average density of Collembola specimens per sampling.

Only in the reference sites there are more forest species than species of open habitats. Number of sylvicolous specimens increases from 1 specimen at the youngest reclamation site **sch-den-5** to 19.6 and 18.7 specimens at the oldest sites **dom-pin-37** and **ple-oak-43**. At the youngest reference site, the average number of forest specimens per sampling was 26.2 and increased rapidly with age to 310.0 specimens at the oldest reference site **alt-oak-00** (fig. 39, tab. 27). Correlation between increase of sylvan specimens and stand age is highly significantly positive ($r = 0.889$, $p < 0.000$), even if the reference sites are excluded ($r = 0.836$, $p < 0.005$). This result is quite similar to that on species level.

The number of specimens typical for open habitats varies strongly: At the youngest reclamation site, 44.0 specimens were found per sampling. The number decreases to 18.6 specimens after 16 years but increases again after 20 years of afforestation. The maximum is reached after 34 years (**koy-oak-34**: 86.0 specimens) where almost two times as many specimens were found as at the youngest reclamation site (fig. 39, tab. 27). But this is most probable a site-specific effect, for most specimens of meadow species occurred in the samples **after** the disturbance by free-cutting immediately to the sampling plot. There is a weak negative correlation to site age ($r = -0.252$, $p < 0.429$) which is not significant. This result is the same if the reference sites are excluded ($r = -0.234$, $p < 0.544$). Without the disturbed site **koy-oak-34**, the

negative correlation becomes stronger, but is still not significant (r = -0.431, p < 0.286). With the disturbed site **koy-oak-34** excluded, a linear diagram would again show the shape of an inverted Ω or a trough, same as we saw at species level. So canopy closure seems to have greatest effect on meadow species.

As average number per sampling, hygrophilous specimens do not play an important role (0 to 2.4 specimens per sampling; fig. 39, tab. 27). There is only a very weak positive correlation to stand age (r = 0.267, p < 0.401) which is not significant, if the reference sites are included. If they are not, there is no correlation between specimens of hygrophilous species and stand age (r = 0.064, p < 0.869). Similar to the results on species level, the reclamation sites do not offer proper habitats for specimens of hygrophilous species.

At the reclamation sites, number of eurotopic specimens per sampling increases with stand age from 1.0 specimen at the youngest site **sch-den-5** to 38.8 and 30.7 at the oldest sites **dom-pin-37** and **ple-oak-43**. At the youngest reference site **alt-oak-29**, there are 3.8 eurotopic specimens at an average per sampling. This number increases to 19.6 at **alt-oak-44** and decreases again at the oldest site **alt-oak-00** to 12.2 (fig. 39, tab. 27). Increase of eurotopic specimens with time is highly significant (r = 0.711, p < 0.010). This is even more so, if the reference sites are excluded (r = 0.895, p < 0.001). As the results are more specific without the reference sites, there must be something special about the oldest reclamation sites.

Other species do hardly occur as an average per sampling (0 to 0.7 specimen; fig. 39, tab. 27).

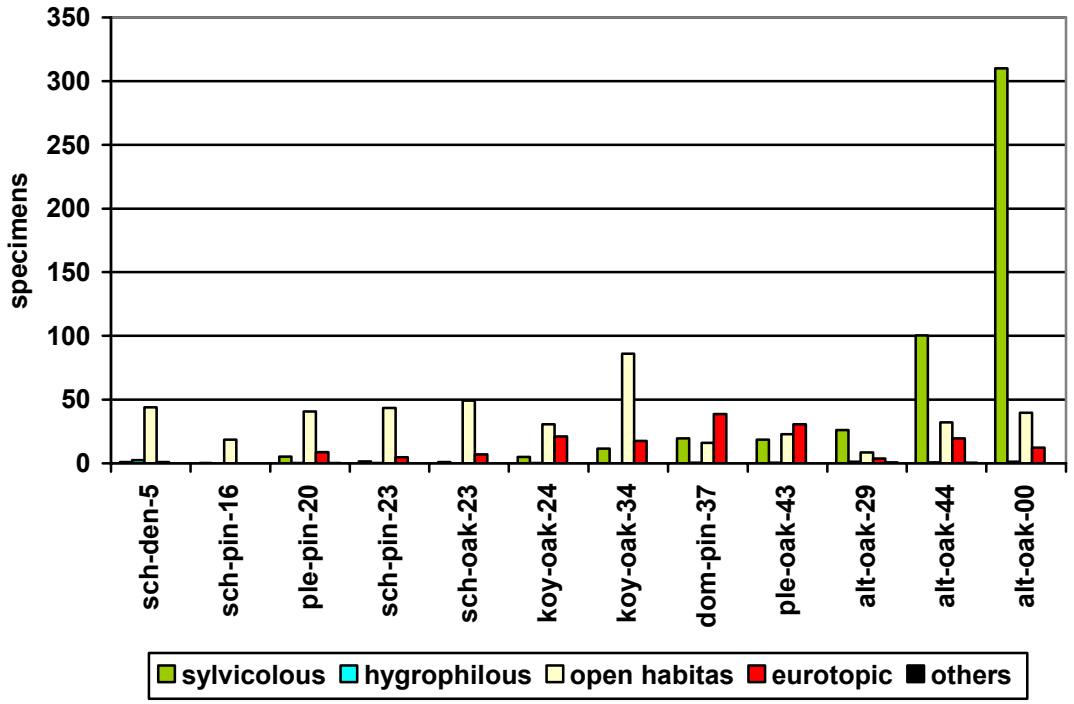


Figure 39: Ecological groups, level of specimens per sampling.

Table 27: Ecological groups, level of specimens per sampling.

	sch-den-5	sch-pin-16	ple-pin-20	sch-pin-23	sch-oak-23	koy-oak-24	koy-oak-34	dom-pin-37	ple-oak-43	alt-oak-29	alt-oak-44	alt-oak-00
sylvicolous	1,0	0,3	5,3	1,6	1,0	5,0	11,5	19,6	18,7	26,2	100,2	310,0
hygrophilous	2,4	0,0	0,3	0,3	0,0	0,2	0,0	0,4	0,4	1,3	0,8	1,2
open habitats	44,0	18,6	40,8	43,6	49,2	30,7	86,0	16,2	22,9	8,5	32,2	39,8
eurotopic	1,0	0,1	8,8	4,9	7,0	21,0	17,5	38,8	30,7	3,8	19,6	12,2
others	0,0	0,0	0,3	0,1	0,0	0,0	0,0	0,0	0,1	0,7	0,4	0,0

Table 28: Correlations of changing numbers of ecological groups (specimens' level) and soil parameters, reference sites are included. Significant positive correlations are marked bright orange, significant negative correlations are marked bright blue.

Altsorgefeld included		forest	hygro	meadow	eurotopic	others
age	Correlation coefficient	0,889	0,267	-0,252	0,711	0,166
	Sig. (2-seitig)	0,000	0,401	0,429	0,010	0,605
	N	12,000	12,000	12,000	12,000	12,000
ph	Correlation coefficient	-0,633	-0,128	0,014	-0,070	-0,306
	Sig. (2-seitig)	0,027	0,693	0,965	0,828	0,334
	N	12,000	12,000	12,000	12,000	12,000
humus	Correlation coefficient	0,904	0,389	-0,294	0,622	0,148
	Sig. (2-seitig)	0,000	0,212	0,354	0,031	0,645
	N	12,000	12,000	12,000	12,000	12,000
conductivity	Correlation coefficient	0,760	0,498	-0,399	0,406	0,250
	Sig. (2-seitig)	0,004	0,099	0,199	0,191	0,433
	N	12,000	12,000	12,000	12,000	12,000
wContent	Correlation coefficient	0,818	0,581	-0,236	0,573	-0,084
	Sig. (2-seitig)	0,002	0,061	0,484	0,066	0,805
	N	11,000	11,000	11,000	11,000	11,000
wCapacity	Correlation coefficient	0,925	0,389	-0,294	0,629	0,148
	Sig. (2-seitig)	0,000	0,212	0,354	0,028	0,645
	N	12,000	12,000	12,000	12,000	12,000
phosphate	Correlation coefficient	-0,361	-0,018	0,172	-0,004	-0,258
	Sig. (2-seitig)	0,248	0,956	0,594	0,991	0,418
	N	12,000	12,000	12,000	12,000	12,000
ammonium	Correlation coefficient	0,848	0,452	-0,084	0,552	0,184
	Sig. (2-seitig)	0,000	0,140	0,795	0,063	0,568
	N	12,000	12,000	12,000	12,000	12,000
nitrate	Correlation coefficient	0,671	0,270	-0,451	0,396	0,463
	Sig. (2-seitig)	0,024	0,423	0,164	0,228	0,151
	N	11,000	11,000	11,000	11,000	11,000
forest	Correlation coefficient	1,000	0,535	-0,340	0,550	0,407
	Sig. (2-seitig)	.	0,073	0,280	0,064	0,189
	N	12,000	12,000	12,000	12,000	12,000
hygro	Correlation coefficient	0,535	1,000	-0,293	-0,025	0,375
	Sig. (2-seitig)	0,073	.	0,355	0,939	0,229
	N	12,000	12,000	12,000	12,000	12,000
meadow	Correlation coefficient	-0,340	-0,293	1,000	-0,175	-0,301
	Sig. (2-seitig)	0,280	0,355	.	0,587	0,342
	N	12,000	12,000	12,000	12,000	12,000
eurotopic	Correlation coefficient	0,550	-0,025	-0,175	1,000	-0,035
	Sig. (2-seitig)	0,064	0,939	0,587	.	0,914
	N	12,000	12,000	12,000	12,000	12,000
others	Correlation coefficient	0,407	0,375	-0,301	-0,035	1,000
	Sig. (2-seitig)	0,189	0,229	0,342	0,914	.
	N	12,000	12,000	12,000	12,000	12,000

Table 29: Correlations of changing numbers of ecological groups (specimens' level) and soil parameters, reference sites are excluded. Significant positive correlations are marked bright orange, significant negative correlations are marked bright blue.

Altsorgefeld excluded		forest	hygro	meadow	eurotopic	others
age	Correlation coefficient	0,836	0,064	-0,234	0,895	0,060
	Sig. (2-seitig)	0,005	0,869	0,544	0,001	0,878
	N	9,000	9,000	9,000	9,000	9,000
ph	Correlation coefficient	-0,151	0,592	-0,435	-0,167	0,055
	Sig. (2-seitig)	0,698	0,093	0,242	0,667	0,888
	N	9,000	9,000	9,000	9,000	9,000
humus	Correlation coefficient	0,820	0,120	-0,100	0,883	-0,060
	Sig. (2-seitig)	0,007	0,759	0,798	0,002	0,879
	N	9,000	9,000	9,000	9,000	9,000
conductivity	Correlation coefficient	0,594	0,291	-0,100	0,533	-0,120
	Sig. (2-seitig)	0,092	0,448	0,798	0,139	0,759
	N	9,000	9,000	9,000	9,000	9,000
wContent	Correlation coefficient	0,738	0,358	-0,143	0,762	-0,385
	Sig. (2-seitig)	0,037	0,384	0,736	0,028	0,346
	N	8,000	8,000	8,000	8,000	8,000
wCapacity	Correlation coefficient	0,870	0,120	-0,100	0,883	-0,060
	Sig. (2-seitig)	0,002	0,759	0,798	0,002	0,879
	N	9,000	9,000	9,000	9,000	9,000
phosphate	Correlation coefficient	0,042	0,419	0,167	0,067	-0,159
	Sig. (2-seitig)	0,915	0,262	0,668	0,865	0,682
	N	9,000	9,000	9,000	9,000	9,000
ammonium	Correlation coefficient	0,736	0,265	0,100	0,717	-0,169
	Sig. (2-seitig)	0,024	0,491	0,798	0,030	0,663
	N	9,000	9,000	9,000	9,000	9,000
nitrate	Correlation coefficient	0,542	0,019	-0,275	0,599	0,190
	Sig. (2-seitig)	0,165	0,965	0,509	0,117	0,652
	N	8,000	8,000	8,000	8,000	8,000
forest	Correlation coefficient	1,000	0,361	-0,259	0,921	0,270
	Sig. (2-seitig)	.	0,340	0,500	0,000	0,482
	N	9,000	9,000	9,000	9,000	9,000
hygro	Correlation coefficient	0,361	1,000	-0,299	0,248	0,301
	Sig. (2-seitig)	0,340	.	0,434	0,520	0,430
	N	9,000	9,000	9,000	9,000	9,000
meadow	Correlation coefficient	-0,259	-0,299	1,000	-0,317	-0,080
	Sig. (2-seitig)	0,500	0,434	.	0,406	0,839
	N	9,000	9,000	9,000	9,000	9,000
eurotopic	Correlation coefficient	0,921	0,248	-0,317	1,000	0,080
	Sig. (2-seitig)	0,000	0,520	0,406	.	0,839
	N	9,000	9,000	9,000	9,000	9,000
others	Correlation coefficient	0,270	0,301	-0,080	0,080	1,000
	Sig. (2-seitig)	0,482	0,430	0,839	0,839	.
	N	9,000	9,000	9,000	9,000	9,000

Dominance of ecological groups (level of specimens per sampling)

Results in total numbers of specimens per sampling equal strongly that of the species level. But if one looks at the changing dominances at the level of specimens, a different picture becomes visible.

The number of forest species increases from 2.1 % and 1.5 % at the youngest reclamation sites **sch-den-5** and **sch-pin-16** to 26.1 % and 25.7 % at the oldest sites **dom-pin-37** and **ple-oak-43**. The increase is more or less linear with the exception of **ple-pin-20**, where site age is considerably older than stand age and 9.5 % are sylvan specimens. Only at **dom-pin-37**, the number of sylvicolous specimens is higher than that of specimens from open habitats. At the youngest reference site **alt-oak-29**, 64.6 % of all specimens were sylvicolous. This amount stays the same for the next 15 years (**alt-oak-44**: 65.4 %) and reaches a climax at the oldest site **alt-oak-00** with 85.4 % of all specimens being sylvicolous (fig. 40, tab. 30). The increase of sylvan specimens is highly significantly correlated to stand age ($r = 0.876$, $p < 0.000$; tab. 31), even if the reference sites are excluded ($r = 0.803$, $p < 0.009$; tab. 32).

Dominance of specimens typical for open habitats declines from about 90.9 % and 97.7 % at the youngest reclamation sites **sch-den-5** and **sch-pin-16** to 74.8 % after 34 years. Their dominance varies strongly in the younger reclamation sites, most probable because of canopy closure. **Sch-oak-23** with a dominance of 81.8 % of meadow specimens is a stand with many gaps on poor soil whereas **koy-oak-24** of about the same age on richer soil has a closer canopy and the dominance of meadow specimens is here only 53.8 %. Although **koy-oak-34** also has a closed canopy, the disturbance by adjacent clear-cutting is visible in an increase in dominance to 74.8 % again. At the 2 oldest reclamation sites **dom-pin-37** and **ple-oak-43**, there is a rapid decrease to 21.6 % and 31.4 % of all specimens being typical for open habitats. At the 2 younger reference sites **alt-oak-29** and **alt-oak-44**, the dominance of specimens from open habitats is 21.0 %. It decreases further to 11.0 % at **alt-oak-00** (fig. 40, tab. 30). The decrease of dominance is significantly correlated to stand age ($r = -0.860$, $p < 0.000$; tab. 31), even if the reference sites are excluded ($r = -0.828$, $p < 0.006$; tab. 32).

Specimens of hygrophilous species are subdominant or recedent only at the youngest reclamation site **sch-den-5** (5.0 %) with its closed herb layer and the youngest reference site **alt-oak-29** (3.3 %) with its cover of *Vaccinium myrtillus* (fig. 40, tab. 30). At all other sites, they are barely subrecedent or missing. A dense vegetation cover seems therefore most important for hygrophilous species. There is no correlation to stand age, no matter if the reference sites are included ($r = -0.066$, $p < 0.839$; tab. 31) or not ($r = -0.056$, $p < 0.887$; tab. 32).

The dominance of eurotopic specimens increases with stand age at the reclamation sites (2.1 % at **sch-den-5** to 42.2 % at **ple-oak-43**). This is not the case with the reference sites, where the dominance of eurotopic specimens seems to decrease with stand age (from 9.5 % at **alt-oak-29** to 3.4 % at **alt-oak-00**; fig. 40, tab. 30). There is only a very weak and not significant positive correlation between dominance of eurotopic specimens and stand age if the reference sites are included ($r = 0.336$, $p < 0.285$; tab. 31). If they are excluded however, there is a significantly high positive correlation ($r = 0.812$, $p < 0.008$; tab. 32).

With a percentage of 0.0 % to 2.0 %, not classified species do not have strong influence on the results (fig. 40, tab. 30).

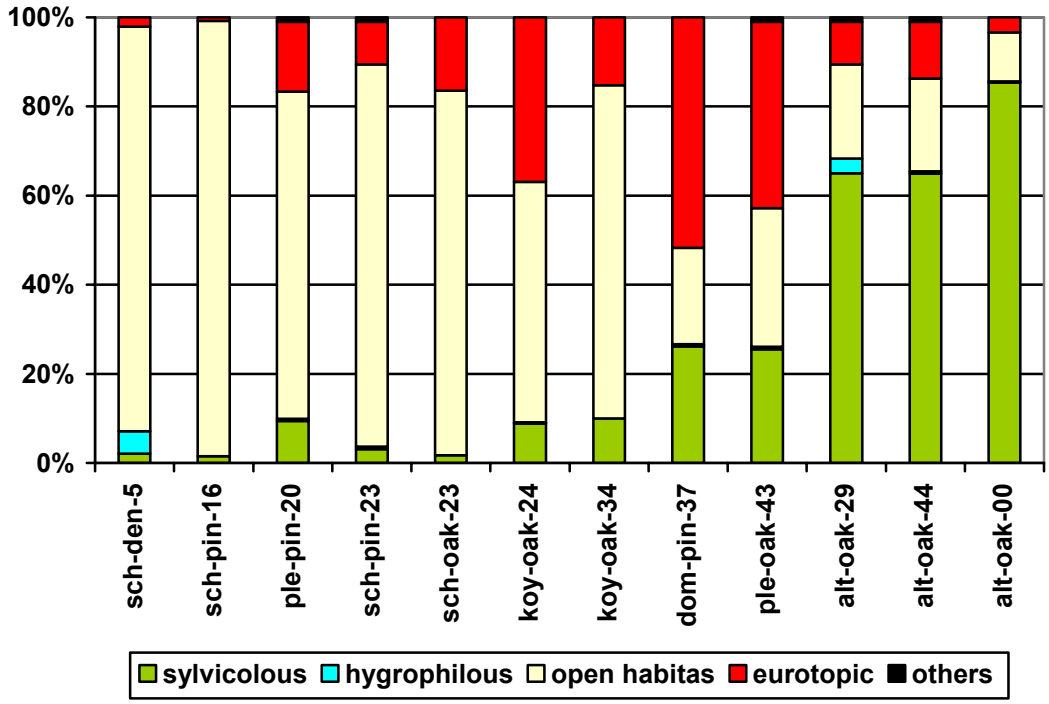


Figure 40: Dominance of ecological groups, level of specimens per sampling.

Analysis of the dominance scale on species level showed, that at the reclamation sites there is a community of meadow species followed by a forest community after about 24 years. On the level of specimens however, we find a community of meadow species for about 34 years which is followed by a community of *eurotopic* species. **Koy-oak-24** with almost 37 % specimens of eurotopic species may suggest that this development begins even earlier, if canopy closure is completed. As already discussed, the older site **Koy-oak-34** was disturbed by clear-cutting with specimens of meadow species invading. Even after more than 40 years, there is no forest community on the level of specimens at the reclamation sites. At the reference sites, even the youngest one **alt-oak-29** is strongly dominated by specimens of forest species (tab. 30).

Table 30: Dominance of ecological groups, level of specimens per sampling. Eudominant groups are marked red.

	sch-den-5	sch-pin-16	ple-pin-20	sch-pin-23	sch-oak-23	koy-oak-24	koy-oak-34	dom-pin-37	ple-oak-43	alt-oak-29	alt-oak-44	alt-oak-00
sylvicolous	2,1	1,5	9,5	3,1	1,7	8,8	10,0	26,1	25,7	64,6	65,4	85,4
hygrophilous	5,0	0,0	0,5	0,6	0,0	0,3	0,0	0,5	0,6	3,3	0,5	0,3
open habitas	90,9	97,7	73,8	86,4	81,8	53,8	74,8	21,6	31,4	21,0	21,0	11,0
eurotopic	2,1	0,8	15,8	9,6	16,4	36,8	15,2	51,7	42,2	9,5	12,8	3,4
others	0,0	0,0	1,0	1,0	0,0	0,0	0,0	0,0	1,0	1,0	1,0	0,0

As indicated above, statistical analysis with Spearman's Rho shows different results, if the sites at Altsorgefeld are included or not. If they are included, there is a highly significant negative correlation between forest species and meadow species ($r = -0.949$, $p < 0.000$) and stand age and meadow species ($r = -0.860$, $p < 0.000$). A highly significant positive correlation is found between stand age and forest species ($r = 0.876$, $p < 0.000$).

Table 31: Correlations of changing dominances of ecological groups (specimens' level) and soil parameters, reference sites are included. Significant positive correlations are marked bright orange, significant negative correlations are marked bright blue.

Altsorgefeld included		forest	hygro	meadow	eurotopic	others
age	Correlation coefficient	0,876	-0,066	-0,860	0,336	0,147
	Sig. (2-seitig)	0,000	0,839	0,000	0,285	0,648
	N	12,000	12,000	12,000	12,000	12,000
ph	Correlation coefficient	-0,614	0,152	0,613	0,158	-0,172
	Sig. (2-seitig)	0,034	0,638	0,034	0,624	0,593
	N	12,000	12,000	12,000	12,000	12,000
humus	Correlation coefficient	0,888	0,018	-0,900	0,329	0,073
	Sig. (2-seitig)	0,000	0,956	0,000	0,297	0,821
	N	12,000	12,000	12,000	12,000	12,000
conductivity	Correlation coefficient	0,762	0,306	-0,697	0,126	0,171
	Sig. (2-seitig)	0,004	0,333	0,012	0,697	0,594
	N	12,000	12,000	12,000	12,000	12,000
wContent	Correlation coefficient	0,818	0,154	-0,747	0,118	-0,173
	Sig. (2-seitig)	0,002	0,652	0,008	0,729	0,611
	N	11,000	11,000	11,000	11,000	11,000
wCapacity	Correlation coefficient	0,916	0,036	-0,893	0,280	0,073
	Sig. (2-seitig)	0,000	0,913	0,000	0,379	0,821
	N	12,000	12,000	12,000	12,000	12,000
phosphate	Correlation coefficient	-0,357	0,091	0,339	0,280	-0,245
	Sig. (2-seitig)	0,254	0,779	0,282	0,378	0,442
	N	12,000	12,000	12,000	12,000	12,000
ammonium	Correlation coefficient	0,853	0,114	-0,764	0,119	0,122
	Sig. (2-seitig)	0,000	0,724	0,004	0,713	0,705
	N	12,000	12,000	12,000	12,000	12,000
nitrate	Correlation coefficient	0,651	0,206	-0,689	0,342	0,389
	Sig. (2-seitig)	0,030	0,543	0,019	0,304	0,237
	N	11,000	11,000	11,000	11,000	11,000
forest	Correlation coefficient	1,000	0,224	-0,949	0,161	0,318
	Sig. (2-seitig)	.	0,484	0,000	0,618	0,313
	N	12,000	12,000	12,000	12,000	12,000
hygro	Correlation coefficient	0,224	1,000	-0,150	-0,089	0,573
	Sig. (2-seitig)	0,484	.	0,642	0,783	0,051
	N	12,000	12,000	12,000	12,000	12,000
meadow	Correlation coefficient	-0,949	-0,150	1,000	-0,273	-0,270
	Sig. (2-seitig)	0,000	0,642	.	0,390	0,396
	N	12,000	12,000	12,000	12,000	12,000

eurotopic	Correlation coefficient	0,161	-0,089	-0,273	1,000	0,073
	Sig. (2-seitig)	0,618	0,783	0,390	.	0,821
	N	12,000	12,000	12,000	12,000	12,000
others	Correlation coefficient	0,318	0,573	-0,270	0,073	1,000
	Sig. (2-seitig)	0,313	0,051	0,396	0,821	.
	N	12,000	12,000	12,000	12,000	12,000

If only the reclamation sites are analyzed, than we find in addition the role of eurotopic species. There are highly significant positive correlations between specimens of eurotopic species and of forest species ($r = 0.733$, $p < 0.025$) and stand age ($r = 0.812$, $p < 0.008$). However, highest negative correlation is found, if the dominance of eurotopic specimens is compared to the dominance of meadow species ($r = -0.950$, $p < 0.000$). So after canopy closure, the conditions for meadow species are no longer favourable but there are also no optimal conditions for forest species yet. In this gap, the community changes into a eurotopic community (tab. 30).

Table 32: Correlations of changing dominances of ecological groups (specimens' level) and soil parameters, reference sites are excluded. Significant positive correlations are marked bright orange, significant negative correlations are marked bright blue.

Altsorgefeld excluded		forest	hygro	meadow	eurotopic	others
age	Correlation coefficient	0,803	-0,056	-0,828	0,812	0,138
	Sig. (2-seitig)	0,009	0,887	0,006	0,008	0,724
	N	9,000	9,000	9,000	9,000	9,000
ph	Correlation coefficient	-0,109	0,472	0,092	-0,067	0,046
	Sig. (2-seitig)	0,781	0,199	0,814	0,864	0,907
	N	9,000	9,000	9,000	9,000	9,000
humus	Correlation coefficient	0,783	-0,051	-0,817	0,850	0,000
	Sig. (2-seitig)	0,013	0,896	0,007	0,004	1,000
	N	9,000	9,000	9,000	9,000	9,000
conductivity	Correlation coefficient	0,600	0,256	-0,433	0,400	0,000
	Sig. (2-seitig)	0,088	0,505	0,244	0,286	1,000
	N	9,000	9,000	9,000	9,000	9,000
wContent	Correlation coefficient	0,738	0,161	-0,619	0,571	-0,282
	Sig. (2-seitig)	0,037	0,704	0,102	0,139	0,499
	N	8,000	8,000	8,000	8,000	8,000
wCapacity	Correlation coefficient	0,850	-0,017	-0,800	0,750	0,000
	Sig. (2-seitig)	0,004	0,965	0,010	0,020	1,000
	N	9,000	9,000	9,000	9,000	9,000
phosphate	Correlation coefficient	0,050	0,248	-0,083	0,200	-0,183
	Sig. (2-seitig)	0,898	0,520	0,831	0,606	0,638
	N	9,000	9,000	9,000	9,000	9,000
ammonium	Correlation coefficient	0,750	0,162	-0,600	0,517	-0,091
	Sig. (2-seitig)	0,020	0,676	0,088	0,154	0,815
	N	9,000	9,000	9,000	9,000	9,000
nitrate	Correlation coefficient	0,491	-0,019	-0,599	0,635	0,190
	Sig. (2-seitig)	0,217	0,965	0,117	0,091	0,652

Altsorgefeld excluded		forest	hygro	meadow	eurotopic	others
	N	8,000	8,000	8,000	8,000	8,000
forest	Correlation coefficient	1,000	0,248	-0,883	0,733	0,274
	Sig. (2-seitig)	.	0,520	0,002	0,025	0,476
	N	9,000	9,000	9,000	9,000	9,000
hygro	Correlation coefficient	0,248	1,000	-0,103	0,043	0,515
	Sig. (2-seitig)	0,520	.	0,793	0,913	0,156
	N	9,000	9,000	9,000	9,000	9,000
meadow	Correlation coefficient	-0,883	-0,103	1,000	-0,950	-0,183
	Sig. (2-seitig)	0,002	0,793	.	0,000	0,638
	N	9,000	9,000	9,000	9,000	9,000
eurotopic	Correlation coefficient	0,733	0,043	-0,950	1,000	0,091
	Sig. (2-seitig)	0,025	0,913	0,000	.	0,815
	N	9,000	9,000	9,000	9,000	9,000
others	Correlation coefficient	0,274	0,515	-0,183	0,091	1,000
	Sig. (2-seitig)	0,476	0,156	0,638	0,815	.
	N	9,000	9,000	9,000	9,000	9,000

So succession is from meadow species to eurotopic species and finally to forest species.

4.2.1.3 Succession of life forms

Species

Highest number of species, both epigaeic and endogaeic, were found at the oldest reference site **alt-oak-00** (21 and 17 species). Lowest number of epigaeic species was found at **sch-den-05** and **sch-oak-23** where only 6 species were recorded. Lowest number of endogaeic species was found at the ash-meliorated site **dom-pin-37** with only 5 species, followed by **sch-pin-16**, which was almost free of litter, with 7 species only (fig. 41, tab. 33).

At both reference sites with *Quercus petraea*, there are about 25 to 35 % more epigaeic than endogaeic species. At sites afforested with *Q. rubra*, there are generally more endogaeic than epigaeic species (fig. 41, tab. 33).

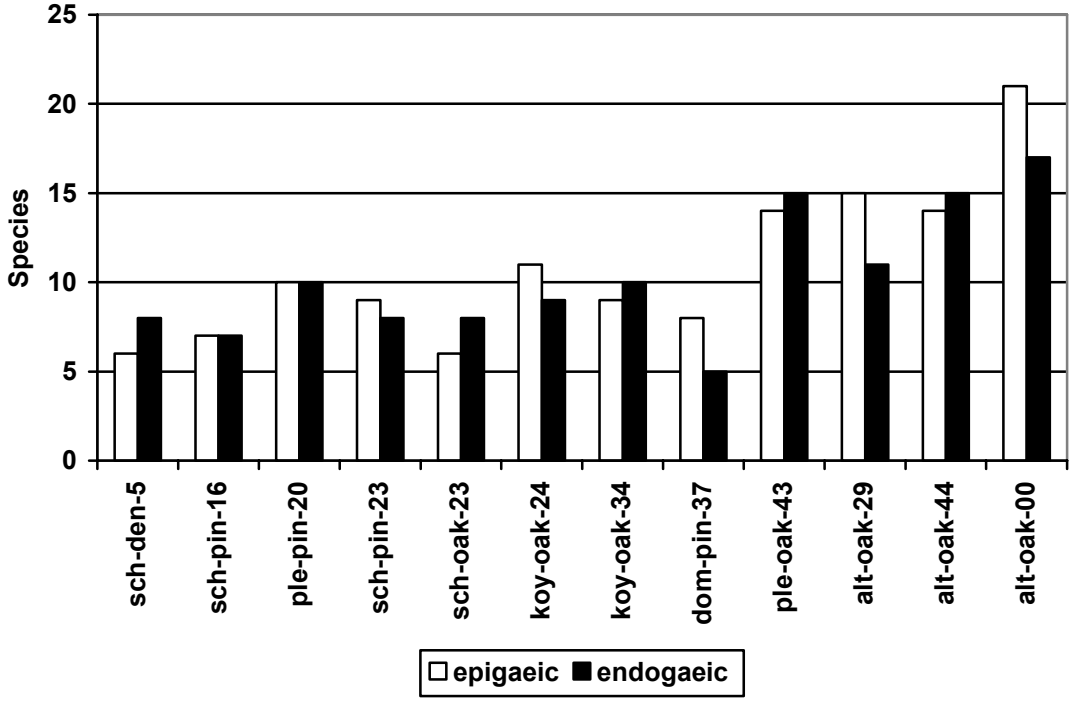


Figure 41: Life forms, species.

Table 33: Life forms, species. *Quercus rubra* stands marked orange, *Q. petraea* stands marked green.

	sch-den-5	sch-pin-16	ple-pin-20	sch-pin-23	sch-oak-23	koy-oak-24	koy-oak-34	dom-pin-37	ple-oak-43	alt-oak-29	alt-oak-44	alt-oak-00
epigaeic	6	7	10	9	6	11	9	8	14	15	14	21
endogaeic	8	7	10	8	8	9	10	5	15	11	15	17

Both life forms are significantly correlated to stand age and ammonium.

Epigaeic species are also significantly positively correlated to organic matter content and water capacity. They are significantly negatively correlated to pH and phosphate. However, if the reference sites are excluded, then there is no significant correlation to these parameters left (tab. 34).

Table 34: Correlations between epigaeic and endogaeic Collembola species and soil properties (Spearman's Rho). Significant positive correlations marked yellow, significant negative correlations marked blue.

Altsorgefeld included	epigaeic		endogaeic		Altsorgefeld excluded	epigaeic		endogaeic	
	r	p	r	p		r	p	r	p
epigaeic	1,000	0,000			epigaeic	1,000	1,000		
endogaeic	0,860	0,000	1,000	0,000	endogaeic	0,717	0,030	1,000	0,000
stand age	0,715	0,009	0,651	0,022	stand age	-0,276	0,472	0,803	0,009
ammonium	0,664	0,018	0,710	0,010	ammonium	0,395	0,293	0,383	0,309
phosphate	-0,586	0,045	-0,324	0,304	phosphate	-0,420	0,230	0,026	0,948
nitrate	0,472	0,142	0,104	0,762	nitrate	0,309	0,456	-0,233	0,578
pH	-0,635	0,027	-0,527	0,079	pH	-0,653	0,057	-0,285	0,458
water content	0,425	0,193	0,325	0,330	water content	0,180	0,670	-0,012	0,977
water capacity	0,661	0,019	0,509	0,091	water capacity	0,445	0,230	0,196	0,614
organic matter	0,615	0,033	0,516	0,086	organic matter	0,328	0,389	0,187	0,629
conductivity	0,478	0,116	0,240	0,452	conductivity	0,185	0,634	-0,136	0,727

Specimens per sampling

Highest average numbers of endogaeic specimens were found at the 2 oldest reference sites **alt-oak-44** (127.6 specimens) and **alt-oak-00** (267.7 specimens). The disturbed site **koy-oak-34** has the highest abundance of endogaeic Collembola of all reclamation sites (81.3). **Sch-pin-16** with its almost bare soil has the lowest abundance of both life forms (fig. 42, tab. 35).

Highest abundances of epigaeic Collembola was found at the oldest reference site **alt-oak-00** (84.0). The increase of endogaeic Collembola is much stronger than that of epigaeic Collembola (fig. 42, tab. 35).

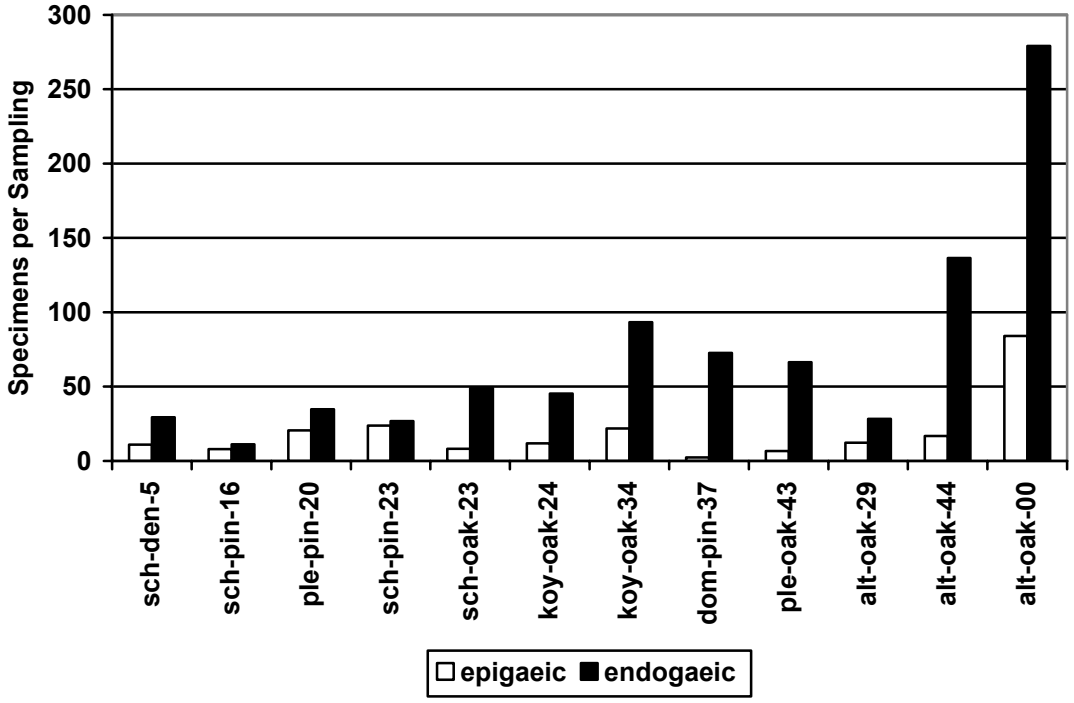


Figure 42: Life forms, specimens per sampling.

Table 35: Life forms, specimens per sampling.

	sch-den-5	sch-pin-16	ple-pin-20	sch-pin-23	sch-oak-23	koy-oak-24	koy-oak-34	dom-pin-37	ple-oak-43	alt-oak-29	alt-oak-44	alt-oak-00
epigaeic	11.0	7.9	20.5	23.7	8.2	11.8	21.7	2.4	6.6	12.3	16.8	84.0
endogaeic	29.3	11.1	34.8	26.7	49.0	45.2	93.3	72.6	66.3	28.2	136.4	279.2

Abundance of epigaeic specimens is significantly negatively correlated to ph ($r = -0.691$, $p < 0.013$) and phosphate ($r = -0.666$, $p < 0.018$). There are no other significant correlations.

Abundance of endogaeic specimens increases significantly with stand age ($r = 0.823$, $p < 0.001$). It is also significantly positively correlated to organic matter content ($r = 0.776$, $p < 0.003$), water content ($r = 0.764$, $p < 0.006$), water capacity ($r = 0.748$, $p < 0.005$) and ammonium ($r = 0.783$, $p < 0.003$). No other significant correlations were found.

If the reference sites are excluded, correlations for epigaeic species are no longer significant. For endogaeic species however, correlations stay significant (tab. 36).

Generally, endogaeic Collembola seem more affected by the analyzed parameters than epigaeic Collembola. The results for the reclamation sites alone indicate that there is a strong development for epigaeic Collembola communities with plant growth, whereas there is less development for endogaeic Collembola communities.

Table 36: Correlations between epigaeic and endogaeic Collembola specimens and soil properties (Spearman's Rho).

Altsorgefeld included	epigaeic		endogaeic		Altsorgefeld excluded	epigaeic		endogaeic	
	r	p	r	p		r	p	r	p
epigaeic	1,000	0,000			epigaeic	1,000	1,000		
endogaeic	0,175	0.587	1,000	0,000	endogaeic	-0,217	0,576	1,000	0,000
stand age	0,172	0,594	0,823	0,001	stand age	-0,276	0,472	0,803	0,009
ammonium	0,280	0,379	0,783	0,003	ammonium	-0,067	0,865	0,800	0,010
phosphate	-0,666	0,018	-0,032	0,923	phosphate	-0,517	0,154	0,300	0,433
nitrate	0,178	0,601	0,246	0,466	nitrate	0,012	0,978	0,263	0,528
pH	-0,691	0,013	-0,361	0,248	pH	-0,653	0,057	-0,285	0,458
water content	0,045	0,894	0,764	0,006	water content	-0,286	0,493	0,810	0,015
water capacity	0,224	0,484	0,748	0,005	water capacity	-0,117	0,765	0,815	0,004
organic matter	0,105	0,746	0,776	0,003	organic matter	-0,333	0,381	0,900	0,001

4.2.1.4 Succession of species

For succession of species, only those species were considered which showed at least some "tendency" or moderate correlation ($p > 0.080 > 0.050$) or significant correlations ($p > 0.050$).

4.2.1.4.1 Succession of epigaeic species

Epigaeic and endogaeic communities were calculated separately as there are obviously different mechanisms working for both communities.

41 epigaeic species were recorded. On the level of dominance of specimens per sampling all species were tested for correlations (Spearman's Rho) to stand age which more or less equals site age. 4 epigaeic species showed moderate correlations to stand age and 5 species significant correlations.

2 species showed a moderate positive correlation to stand age: *Arrhopalites caecus* ($r = 0.533$, $p < 0.074$); *Neanura muscorum* ($r = 0.533$, $p < 0.074$).

4 species showed a significant positive correlation to age: *Entomobrya corticalis* ($r = 0.641$, $p < 0.025$); *Micraphorura absoloni* ($r = 0.625$, $p < 0.030$); *Orchesella flavescens* ($r = 0.724$, $p < 0.008$); *Pseudachorutes parvulus* ($r = 0.641$, $p < 0.025$).

All six of them are forest species.

2 species have a moderate negative correlation to stand age: *Entomobrya multifasciata* (r = -0.533, p < 0.062), *Paratullbergia macdougalli* (r = -0.575, p < 0,051).

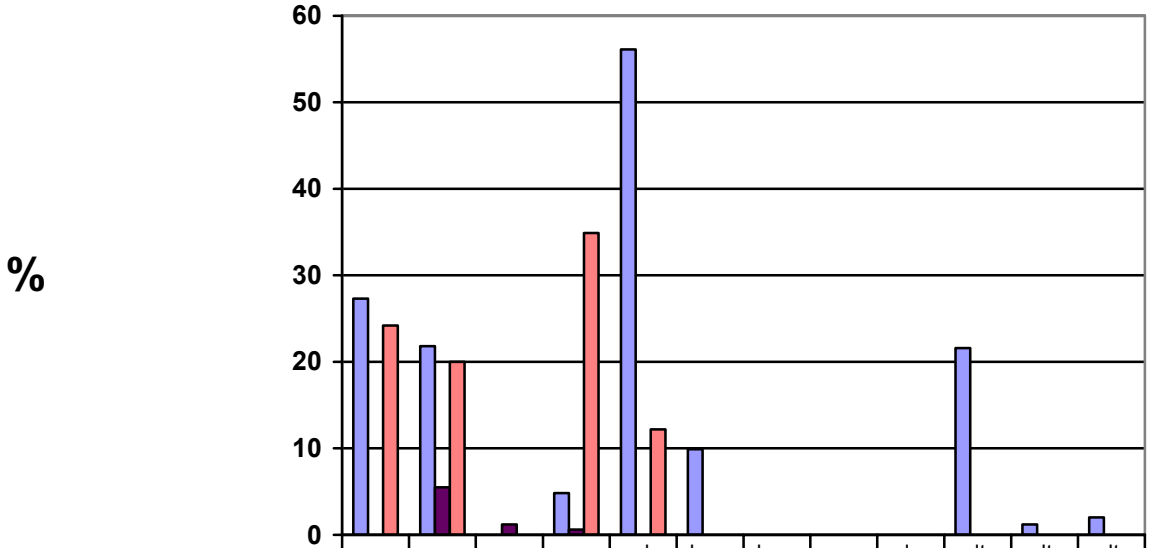
1 species has a significant negative correlation to stand age: *Schoetella ununguiculata* (r = -0.704, p < 0.011).

All 3 species with negative correlations are species of open habitats.

Development of moderately and significantly correlated species, which are at least subdominant in one site, is studied in more detail.

Dominance of specimens per sampling

The dominance scale of 3 species with negative correlation to stand age shows that *Paratullbergia macdougalli* and *Schoetella ununguiculata* are absent after canopy closure and missing at the reference sites. *Entomobrya multifasciata* is also missing in the older reclamation sites, but is the eudominant species at **sch-oak-**23 and found in all reference sites, especially at the youngest one where it is one of the dominant epigaeic species. *P. macdougalli* is also missing at the youngest reclamation site which is covered by dense vegetation. It was only found at sites with bare soil or covered by pine needles of younger stands. At **ple-pin-20** *E. multifasciata* and *Sch. ununguiculata* are both missing (fig. 43).



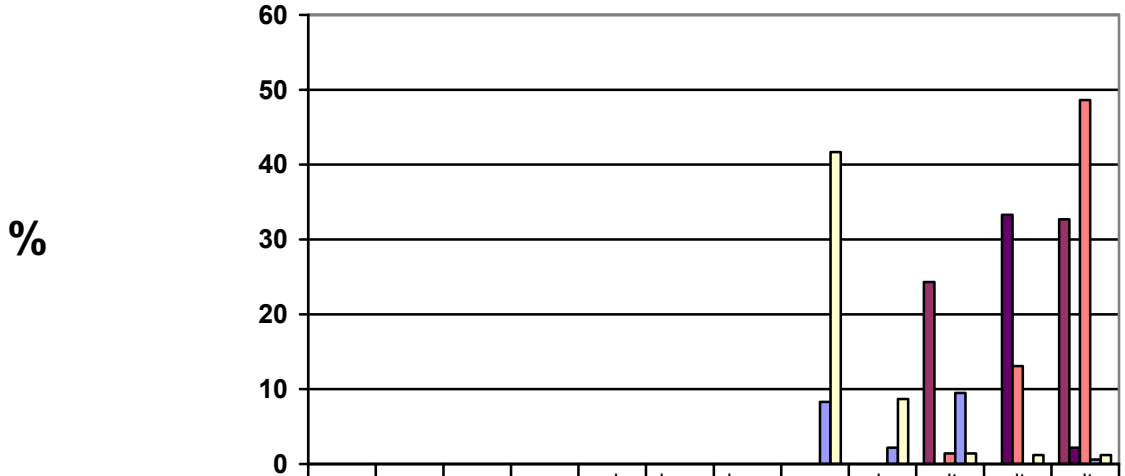
	sch-den-5	sch-pin-16	ple-pin-20	sch-pin-23	sch-oak-23	koy-oak-24	koy-oak-34	dom-pin-37	ple-oak-43	alt-oak-29	alt-oak-44	alt-oak-00
Entomobrya muiltifasciata	27,3	21,8	0	4,8	56,1	9,9	0	0	0	21,6	1,2	2
Paratullbergia macdougalli	0	5,5	1,2	0,6	0	0	0	0	0	0	0	0
Schoetella ununguiculata	24,2	20	0	34,9	12,2	0	0	0	0	0	0	0

Figure 43: Dominance scale of epigaeic species with a negative correlation to stand age, only species which are at least subdominant once.

Of the 5 species with positive correlations, 3 are exclusively found at the reference sites: *Anurophorus atlanticus, Micraphorura absoloni* and *Entomobrya corticalis*. The last species was only found at the older reference sites.

A. atlanticus was not found at the *Quercus rubra* stand **alt-oak-44** but is a dominant epigaeic species at both *Q. petraea* stands. *M. absoloni* becomes eudominant at the oldest reference site.

Neanura muscorum was found at the older reclamation sites as well as at the reference sites with the exception of **alt-oak-44**. *Orchesella flavescens* is eudominant at **dom-pin-37** but much less dominant at sites with *Quercus* stands (fig. 44).



	sch-den-5	sch-pin-16	ple-pin-20	sch-pin-23	sch-oak-23	koy-oak-24	koy-oak-34	dom-pin-37	ple-oak-43	alt-oak-29	alt-oak-44	alt-oak-00
Anurophorus atlanticus	0	0	0	0	0	0	0	0	0	24,3	0	32,7
Entomobrya corticalis	0	0	0	0	0	0	0	0	0	0	33,3	2,2
Micraphorura absoloni	0	0	0	0	0	0	0	0	0	1,4	13,1	48,6
Neanura muscorum	0	0	0	0	0	0	0	8,3	2,2	9,5	0	0,6
Orchesella flavescens	0	0	0	0	0	0	0	41,7	8,7	1,4	1,2	1,2

Figure 44: Dominance scale of epigaeic species with positive correlations to stand age, only species which are at least subdominant once.

4.2.1.4.2 Succession of endogaeic species

26 endogaeic species were recorded. All species were tested (Spearman's Rho) for correlation between changes in dominance and (stand) age.

5 showed a significant positive correlation to stand age ($p = 0.050$ to 0.000): *Folsomia penicula* ($r = 0.727$, $p < 0.007$), *Friesea mirabilis* ($r = 0.690$, $p < 0.013$), *Isotomiella minor* ($r = 0.737$, $p < 0.006$), *Metaphorura affinis* ($r = 0.641$, $p < 0.025$), *Protaphorura armata* ($r = 0.692$, $p < 0.013$).

2 species showed a significant negative correlation ($p = 0.050$ to 0.000): *Mesaphorura atlantica* ($r = -0.642$, $p < 0.024$), *Mesaphorura macrochaeta* ($r = -0.680$, $p < 0.015$).

1 more species showed a tendency (p = 0.080 to 0.050) to be found at older sites: *Folsomia candida* (r = 0.543, p < 0.068).

The other 18 species showed no such significances or tendencies: *Folsomia fimetaria* (r = 0.423, p < 0.171)*, Folsomia quadrioculata* (r = 0.471, p < 0.122)*, Megalothorax minimus* (r = 0.481, p < 0.113)*, Mesaphorura critica* (r = 0-0.406, p < 0.190)*, Mesaphorura hylophila* (r = -0.384, p < 0.218)*, Mesaphorura tenuisensillata* (r = -0.481, p < 0.113), *Mesaphorura yosii* (r = 0.481, p < 0.113)*, Micranurida pygmea* (r = -0.321, p < 0.309)*, Microanurophorus music* (r = -0.306, p < 0.333)*, Parisotoma notabilis* (r = 0.256, p < 0.422), *Proisotoma minuta* (r = 0.051, p < 0.874)*, Protaphorura meridiata* (r = 0.438, p < 0.154)*, Pseudoanurophorus alticolus* (r =-0.175, p < 0.586)*, Pseudosinella alba* (r = 0.394, p < 0.205)*, Vertagopus arboreus* (r = -0.182, p < 0.571)*, Willemia anophthalma* (r = 0.312, p < 0.323)*, Willemia aspinata* (r = 0.131, p < 0.684)*, Willemia intermedia* (r = 0.219, p < 0.495)*.*

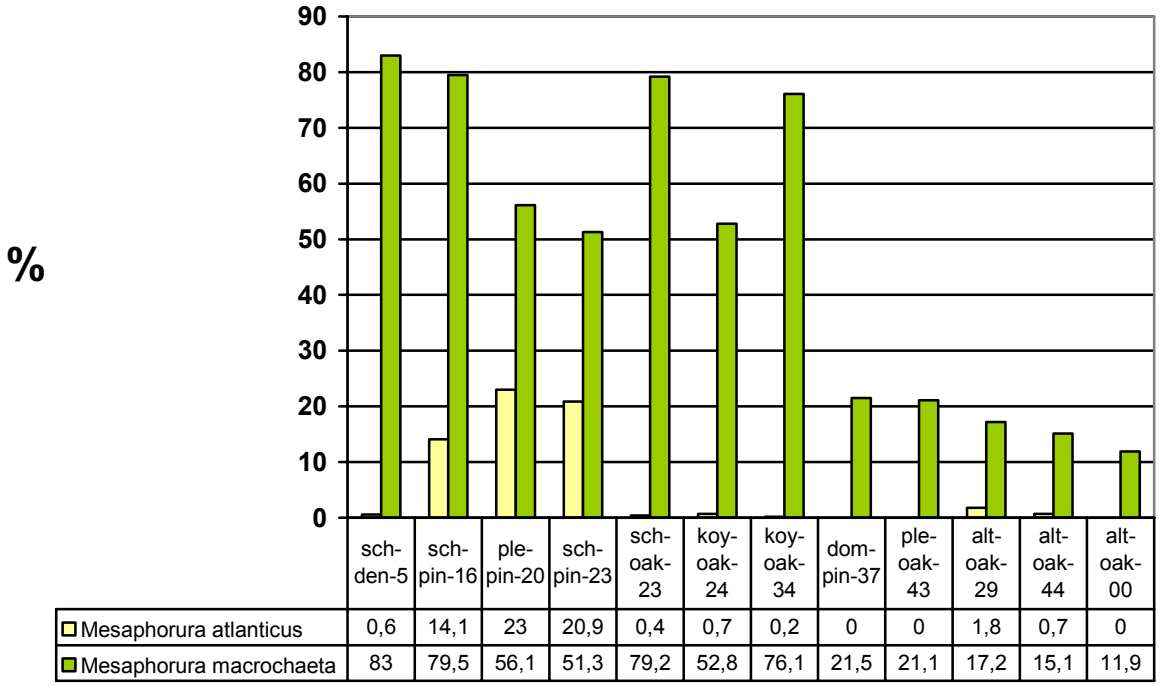
Development of significantly correlated species and those showing tendencies was studied in more detail if these species were at least subdominant at one site.

Changes in dominance of selected species

Endogaeic species

2 species were found with significant negative correlations and being at least subdominant once. *Mesaphorura atlanticus* is dominant at the early stages of pine afforestation. The sites **sch-pin-16, ple-pin-20** and **sch-pin-23** are characterised by young pine stands and a lack of herb layers. There is just bare sand covered to some degrees with pine needles. The species is recedent or missing in older sites where soil is covered by litter. It is as well recedent in **sch-den-5** with its dense vegetation cover.

M. macrochaeta was found at all sites with dominances of at least 12 %. Dominance is decreasing however from the younger reclamation sites with about 50 to 80 % dominance to 20 to 12 % at the older reclamation sites and all reference sites. It is eudominant at all reclamation sites, but there is a breakdown in dominance from **koy-oak-34** to **dom-pin-37** from 76.1 % to 21.1 %. This observation will have to be discussed later (fig. 45).



	sch-den-5	sch-pin-16	ple-pin-20	sch-pin-23	sch-oak-23	koy-oak-24	koy-oak-34	dom-pin-37	ple-oak-43	alt-oak-29	alt-oak-44	alt-oak-00
Mesaphorura atlanticus	0,6	14,1	23	20,9	0,4	0,7	0,2	0	0	1,8	0,7	0
Mesaphorura macrochaeta	83	79,5	56,1	51,3	79,2	52,8	76,1	21,5	21,1	17,2	15,1	11,9

Figure 45: Dominance scale of endogaeic species with a significant negative correlation to stand age, only species which are at least subdominant once.

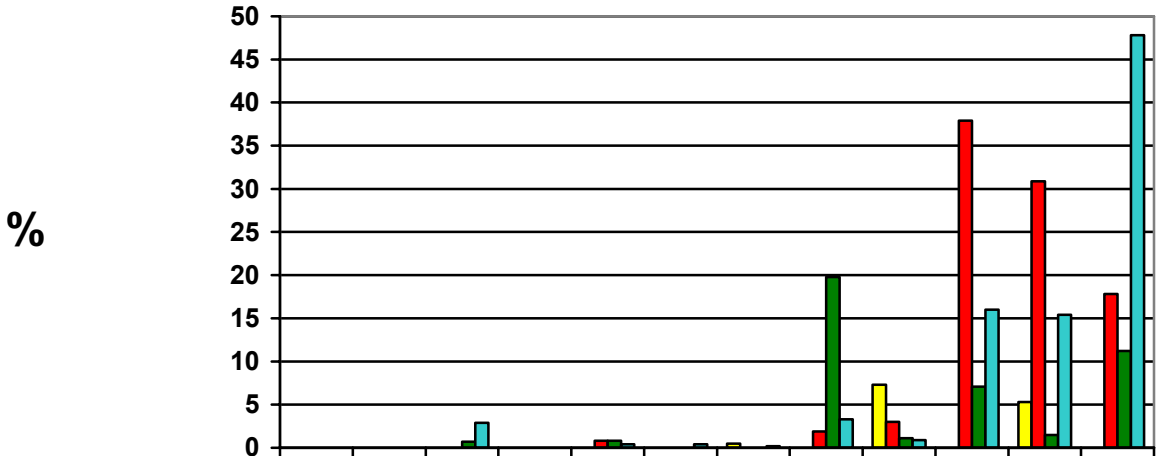
3 species were found with significant positive correlations to stand age and one showed a strong tendency (*Folsomia candida*).

Folsomia candida was only found in *Quercus rubra* stands. It never occurred in any pine or *Quercus petraea* stand.

The forest species *Folsomia penicula* was recorded only once from reclaimed land less than 37 years old (**sch-pin-23**) as subrecedent species. Only at the two oldest reclamation sites *F. penicula* becomes subdominant. At the reference sites however, it is at least a dominant species, at **alt-oak-29** almost eudominant

The eurotopic species *Friesea mirabilis* ($r = 0.690$, $p < 0.013$) is missing at most reclamation sites. It is subrecedent at **sch-pin-16** and **sch-pin-23** and recedent at the oldest reclamation site **ple-oak-43**. At the ash-meliorated site **dom-pin-37** however, *F. mirabilis* is a eudominant species. At the reference sites, the species is dominant at the youngest and the oldest site, but only recedent at **alt-oak-44**, which is a *Quercus rubra* stand (fig. 46).

The forest species *Isotomiella minor* was recorded from all stands older than 23 years. At the reclamation sites it is a recedent and subrecedent species with the exception of the ash-meliorated site **dom-pin-37** where *I. minor* is subdominant. At all reference sites, it is dominant and even eudominant at the oldest site (fig. 46).



	sch-den-5	sch-pin-16	ple-pin-20	sch-pin-23	sch-oak-23	koy-oak-24	koy-oak-34	dom-pin-37	ple-oak-43	alt-oak-29	alt-oak-44	alt-oak-00
Folsomia candida	0	0	0	0	0	0	0,5	0	7,3	0	5,3	0
Folsomia penicula	0	0	0	0	0,8	0	0	1,9	3	37,9	30,9	17,8
Friesea mirabilis	0	0	0,7	0	0,8	0	0	19,8	1,1	7,1	1,5	11,2
Isotomiella minor	0	0	2,9	0	0,4	0,4	0,2	3,3	0,9	16	15,4	47,8

Figure 46: Dominance scale of endogaeic species with significant positive correlations or strong positive tendencies to stand age, only species which are at least subdominant once.

4.2.1.5 Cluster analysis

Cluster analysis for similarities of specimens (Pearson correlation coefficient, Ward minimum variance method) distinguishes two main groups: Young soils at the reclamation sites and “old”, undisturbed soils at the reference sites at Altsorgefeld. Reclamation sites show high dominances (generally eudominance) of *Mesaphorura macrochaeta*. The sites of Altsorgefeld are dominated by *Folsomia penicula* and *Isotomiella minor*. At **alt-oak-00**, the latter one is eudominant.

Reclamation sites are further subdivided into 3 subgroups. The first is defined by *Parisotoma notabilis* which is the (eu)dominant species at (**dom-pin-37** and **ple-oak-43**). At **koy-oak-24**, *M. macrochaeta* ist he dominant species with *P. notabilis* almost being eudominant. The next subgroup is made of the two pine woods **sch-pin-23** and **ple-pin-20**. Here, we have *M. atlantica* as a dominant species with *M. macrochaeta* being eudominant. The last group is made of 4 sites. Its pine site **sch-pin-16** is again a *M. macrochaeta – M. atlantica* community, but *M. macrochaeta* is even more dominant now. The 3 other sites are dominated by *M. macrochaeta* with values > 76 % in the edaphic community (fig. 47).

It is very interesting to note, that the cluster tree can be explained by using only the edaphic community!

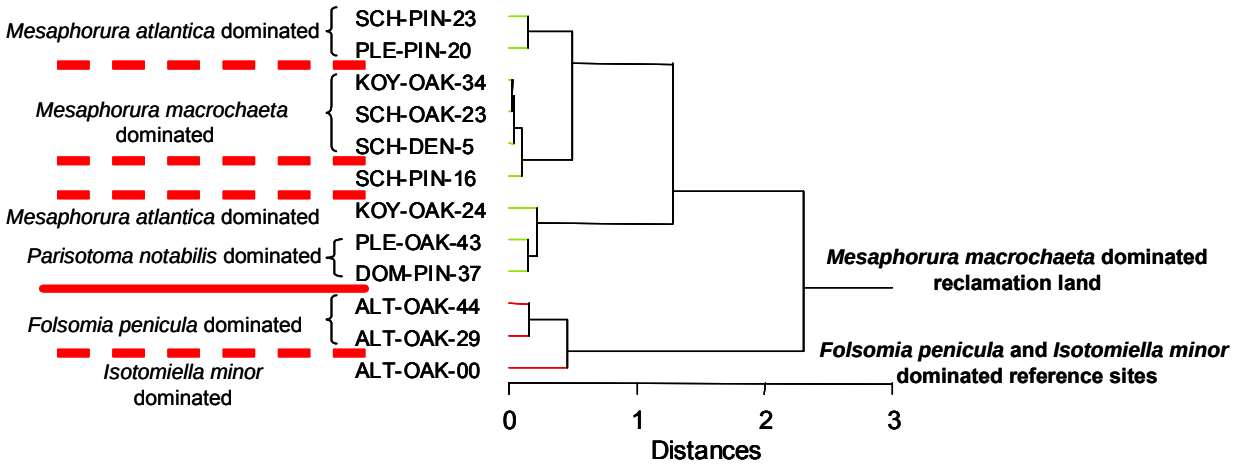


Figure 47: Cluster analysis of Collembola communities of afforested sites (Distance metric is 1-Pearson correlation coefficient, Ward minimum variance method).

Table 37: Distance metric is 1-Pearson correlation coefficient, Ward minimum variance method

Cluster Containing	and cluster containing	were joined at distance	No. of members in new cluster
KOYOAK34	SCHOAK23	0.025	2
KOYOAK34	SCHDEN5	0.043	3
KOYOAK34	SCHPIN26	0.103	4
PLEOAK43	DOMPIN37	0.146	2
SCHPIN23	PLEPIN20	0.147	2
ALTOAK44	ALTOAK29	0.161	2
KOYOAK24	PLEOAK43	0.215	3
ALTOAKoo	ALTOAK44	0.456	3
KOYOAK34	SCHPIN23	0.496	6
KOYOAK34	KOYOAK24	1.276	9
ALTOAK00	KOYOAK34	2.305	12

4.2.2 Sites with free succession

The sites with free succession were classified into 3 main vegetation structures: 3 dunes and sites with bare substrate, 5 sites with sparse vegetation (xeric grasslands) and 8 sites with dense vegetation (mainly *Calamagrostis epigejos* dominated). 3 reference sites were also studied, one with sparse vegetation and two with dense vegetation.

In the chronosequence of the afforested sites, structure changes continuously with age. Therefore, there is no need to separate structure from site age. But in contrast to the afforested sites, a simple chronosequence, arranged only after the age of sites is not sufficient for the complex pattern of structure of the sites with free succession. Number of species would vary randomly between 3 and 32 species in the reclamation sites (fig. 49) and density of specimens would decrease with age of sites (fig. 48). Simple chronosequences exclude the fact that Collembola communities reflect the development of vegetation (e.g. PARSONS & PARKINSON 1986, SLAWSKA 1997).

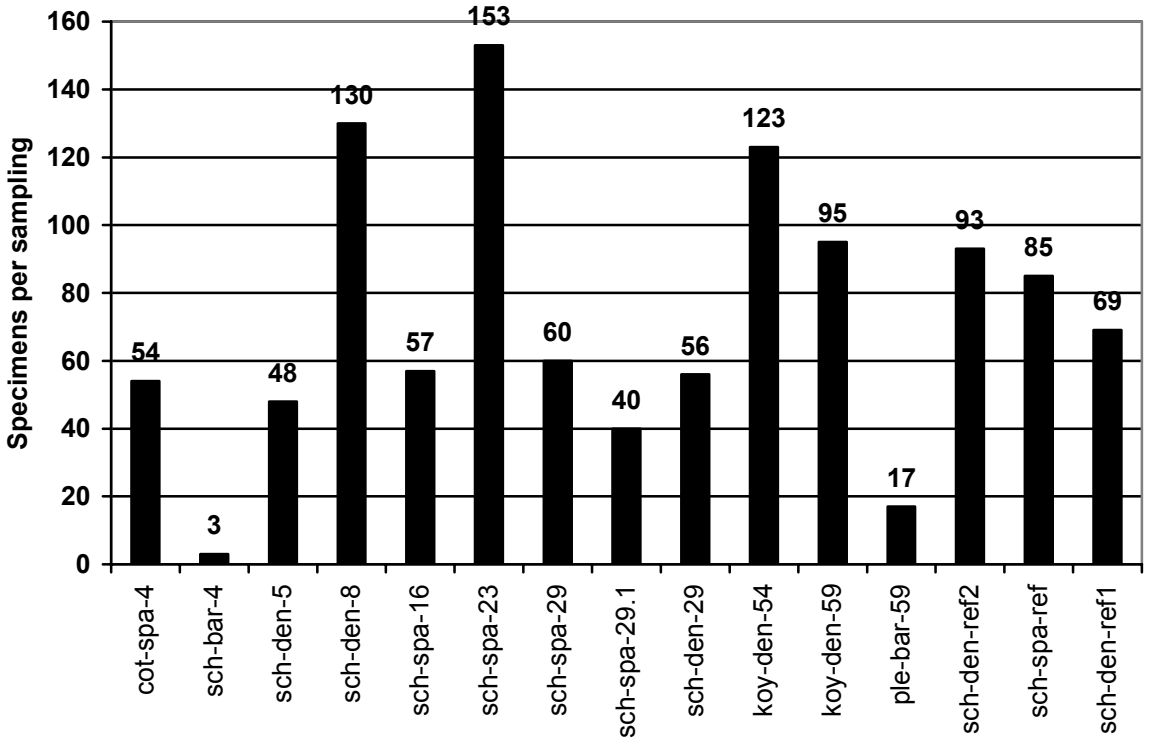


Figure 48: Simple chronosequence without considering vegetation structure (specimens per sampling).

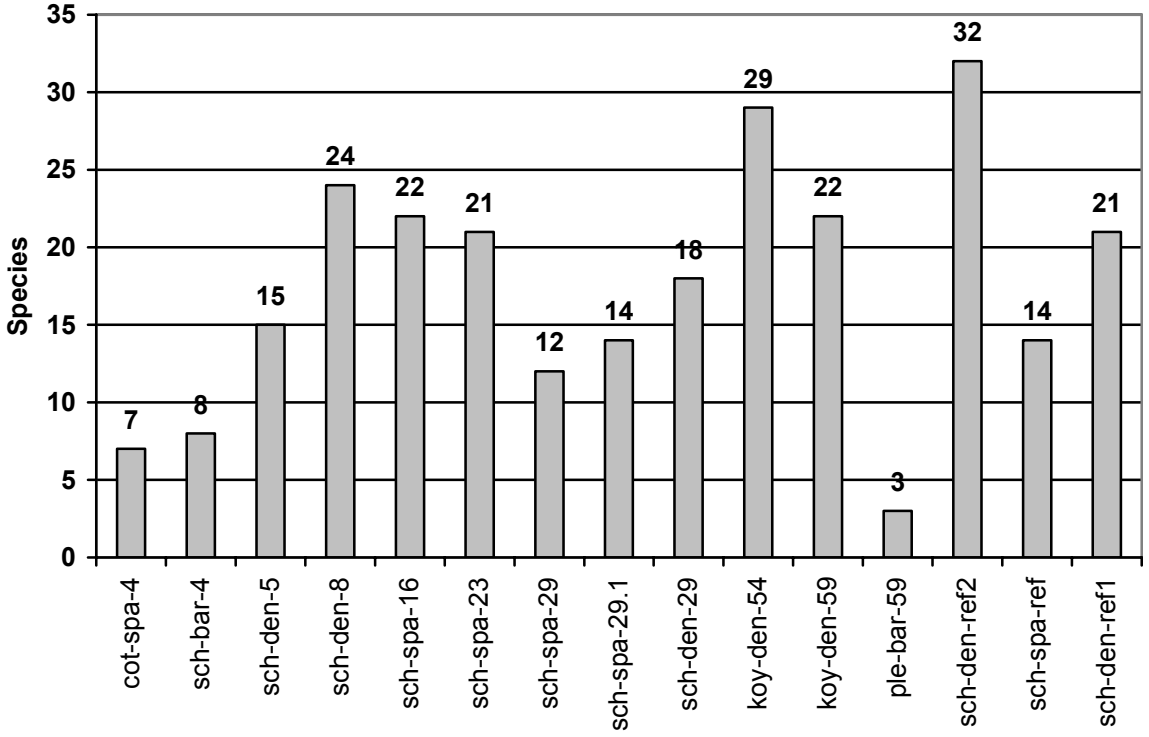


Figure 49: Simple chronosequence without considering vegetation structure (species number).

Spearman-Rho does not show any correlation between site age and number of specimens per sampling ($r = 0.216$, $p < 0.501$) or site age and number of species ($r = 0.189$, $p < 0.556$) if the chronosequence is arranged simply by age of sites (tab. 38). Only the reclamation sites were tested as one cannot call the reference sites a certain age.

Table 38: Correlations between site age, specimens per sampling and species, only reclamation sites.

			Site age	specimens	species
Spearman's Rho	Site age	Correlation Coefficient r	1,000	,216	,189
		Sig. (2-tailed) p	.	,501	,556
		N	12	12	12
	specimens	Correlation Coefficient	,216	1,000	,774(**)
		Sig. (2-tailed)	,501	.	,003
		N	12	12	12
	species	Correlation Coefficient	,189	,774(**)	1,000
		Sig. (2-tailed)	,556	,003	.
		N	12	12	12

** Correlation is significant at the 0.01 level (2-tailed).

Therefore, a modified chronosequence regarding the vegetation structure was used: The chronosequence is divided into 3 sub-chronosequences reflecting the main vegetation structures

1. bare substrate (sand, dunes)
2. sparse vegetation (vegetation cover 10 % - 70 %)
3. dense vegetation (vegetation cover > 70 %)

These 3 parts were arranged according to their age with the reference site(s) as the “oldest” sites within the sub-chronosequences. So the x-axis does not only show the age of a certain site but also its structure in terms of linear succession of vegetation. This results in a structural chronosequence.

4.2.2.1 Species composition and dominance scale

7.607 specimens, distributed across 84 species were identified in 19 sites. Abundance and species richness increase with structure and age of sites (fig. 50, fig. 51).

At the youngest site with bare substrate, 8 species were found. 9 species were found at the older site, but number of species decreases at the oldest site (3).

It increases considerably from the youngest site with sparse vegetation (7 species) to the older sites and reaches a level of 11 to 15 species.

At sites with dense vegetation, species number varies from 15 species at the youngest site to 32 species at the second reference site. The increase is not continuous like at the sites with sparse vegetation but varies strongly. The highest number of species at reclamation sites is found at the littoral site (24 species) and at the second oldest site (29 species).

Number of specimens per sampling varies similarly to that of the number of species. At the youngest dune it increases ten times to the older site. At the oldest dune, it decreases to half its former level. The number of specimens in sites with sparse vegetation varies between 36 at the second youngest site and 85 at the reference site.

At sites with dense vegetation, number of specimens per sampling varies strongly between 48 and 153.

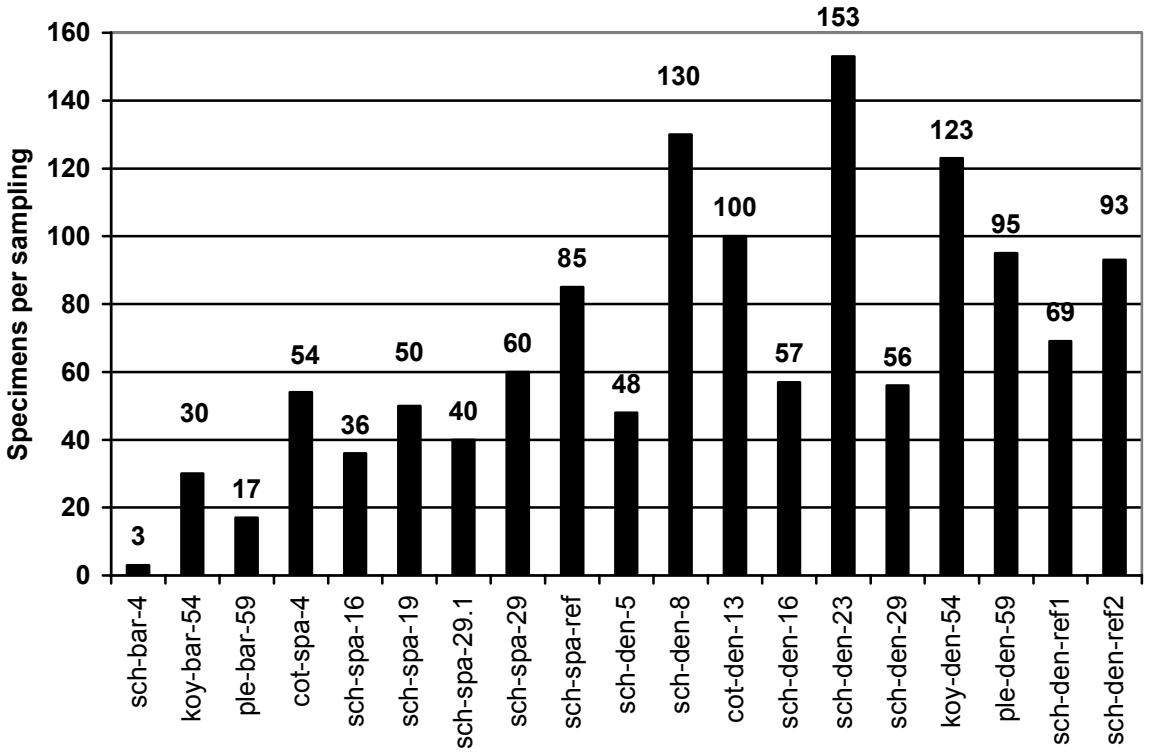


Figure 50: Structural chronosequence following vegetation structure and site age (specimens per sampling).

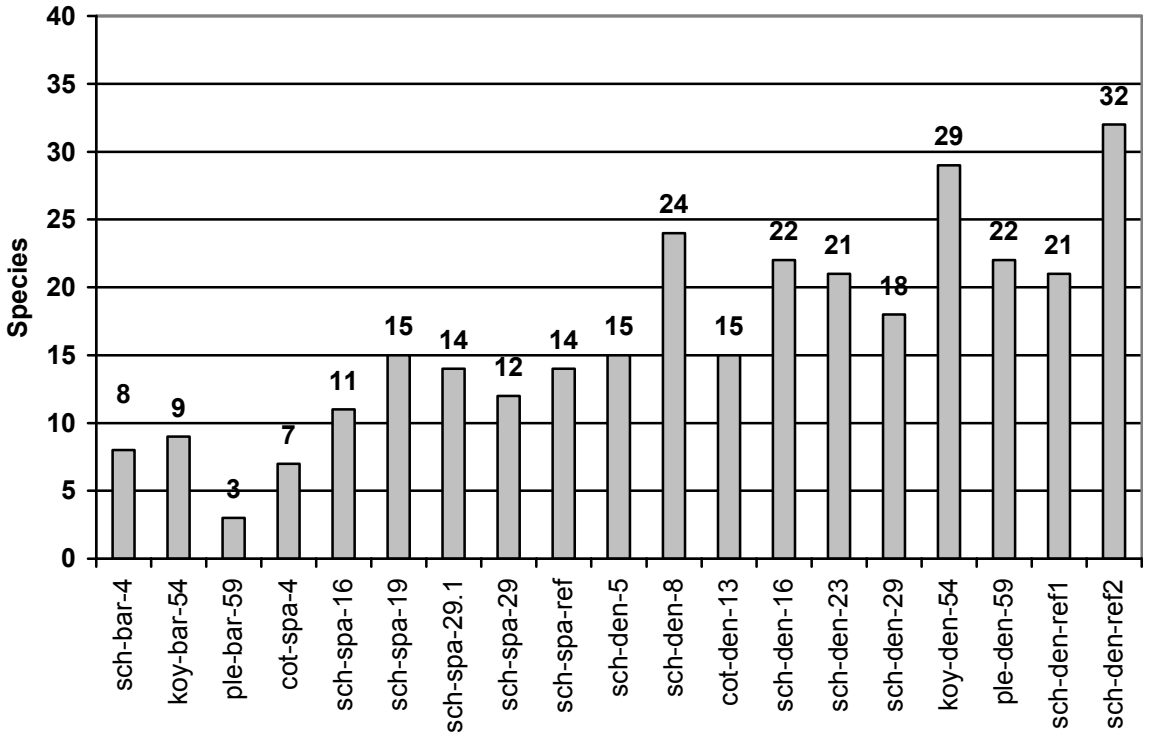


Figure 51: Structural chronosequence following vegetation structure and site age (species number).

Now Spearman-Rho shows a significantly positive correlation between structure and number of specimens per sampling (r = 0.767, p < 0.000) and structure and number of species (r = 894, p < 0.000, tab. 39).

Table 39: Correlations between structure/age, specimens per sampling and species. All sites. Using the structural chronosequence, highly significant correlations show up.

			structure	specimens	species
Spearman-Rho	structure	Correlation coefficient	1,000	,767(**)	,894(**)
		Sig. (2-seitig)	.	,000	,000
		N	19	19	19
	specimens	Correlation coefficient	,767(**)	1,000	,767(**)
		Sig. (2-seitig)	,000	.	,000
		N	19	19	19
	species	Correlation coefficient	,894(**)	,767(**)	1,000
		Sig. (2-seitig)	,000	,000	.
		N	19	19	19

** Correlation is significant on the 0,01 level.

Dominance

Sites without vegetation are dominated by *Mesaphorura macrochaeta* and *M. atlantica*. *M. macrochaeta* is eudominant, *M. atlantica* dominant. However, both species differ only slightly (46.3 % and 35.5%) and *M. atlantica* is present at every sampling whereas *M. macrochaeta* is present only at 2 of the three sites. All other species are recedent and subrecedent. With only 203 specimens in all 3 sites, species with only 1 or 2 specimens are automatically regarded as recedent and subrecedent.

Sites with sparse vegetation are also dominated by *Mesaphorura macrochaeta* and *M. atlantica*, but both species are only dominant and less abundant (28.3 % and 17.9 %). As dominant species they are joined by *Pseudoanurophorus alticolus* (15.3 %). *Proisotoma minuta* (8.2 %) and *Mesaphorura critica* (7.0 %) are subdominant species. 8 more species are recedent and 17 others subrecedent.

In sites with dense vegetation, *Parisotoma notabilis* dominates (32.1 %) the community. A second dominant species is *Mesaphorura macrochaeta* (18.5 %). *Isotoma anglicana* and *Entomobrya multifasciata* are subdominant species (6.5 % and 4.5 %). 10 species are recedent and 53 species subrecedent.

5 species are missing in the 16 reclamation sites: *Lepidocyrtus paradoxus*, *Mesaphorura italica*, *Orchesella villosa*, *Sminthurides malmgreni* and *Sminthurus viridis*.

In contrast, 28 species were not recorded from the 3 reference sites: *Anurophorus atlanticus, Ceratophysella denticulata, Cyphoderus albinus, Desoria violacea, Entomobrya lanuginose, Folsomia dovrensis, Folsomia manolachei, Folsomia onychiurina, Heteromurus nitidus, Hypogastrura manubrialis, Mesaphorura*

tenuisensillata, Metaphorura affinis, Micraphorura absoloni, Neanura muscorum, Orchesella bifasciata, Orchesella cincta, Orchesella flavescens, Proisotoma minima, Protaphorura meridiata, Pseudachorutes subcrassus, Pseudosinella octopunctata, Schoetella ununguiculata, Seira domestica, Tomocerus vulgaris, Vertagopus arboreus, Willemia anophthalma, Willemia aspinata, Willemia intermedia.

The 16 reclamation sites are dominated by *Parisotoma notabilis* (25.8 %) and *Mesaphorura macrochaeta* (22.7 %) as dominant species. 4 species are subdominant: *Isotoma anglicana* (6.4 %), *Proisotoma minuta* (4.7 %), *Entomobrya multifasciata* (4.7 %), *Mesaphorura atlantica* (4.0 %; fig. 52). 7 Species are recedent and 54 species subrecedent.

The 3 reference sites are dominated by *Mesaphorura macrochaeta* (16.8 %), *Pseudoanurophorus alticolus* (15.9 %) and *Parisotoma notabilis* (12.8 %) as dominant species. *Mesaphorura critica* is the only subdominant species (7.6 %). 13 species are recedent and 27 species subrecedent (fig. 52).

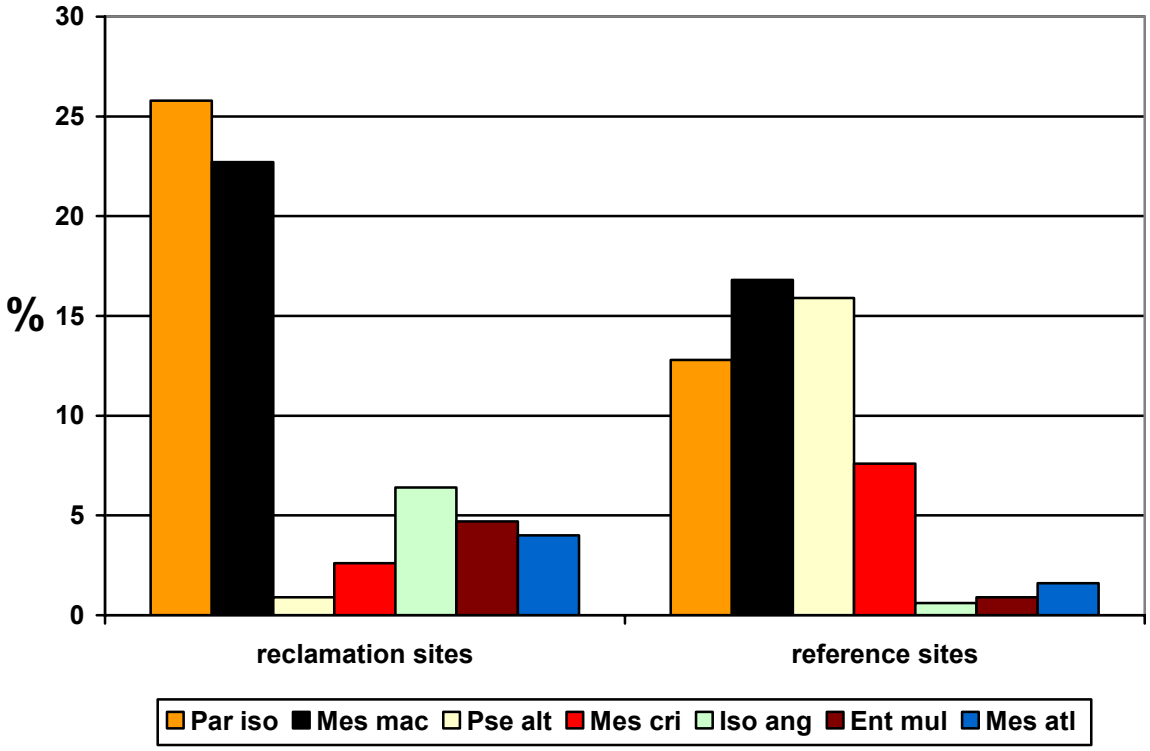


Figure 52: Dominances on reclamation sites and reference sites (dominant and subdominant species).

4.2.2.2 Succession of ecological groups

Species, absolute numbers

In total numbers, species of open habitats are constantly present with numbers between 9 (6) and 14. Exceptions are **ple-bar-59** with only 2 species and the second reference site with 17 species. Their increase with structure is significant ($r = 0.60$, $p < 0.011$).

Number of sylvan species increases with time and structure. Only 1 species was recorded from the youngest dune and none from the older dunes. At sites with sparse vegetation, sylvan species are more common. At half of these sites, 1 to 4 forest species are present. However, they are missing at the two youngest sites and **sch-spa-29.1**. Constantly present are forest species at sites with dense vegetation. At the two oldest reclamation sites, 9 and 8 species were recorded. There is a gap between the oldest reclamation site and the reference sites, at **sch-den-ref1** only 2 and at **sch-den-ref2** 5 species were recorded. Increase of sylvan species is highly correlated to structure ($r = 0.76$, $p < 0.000$).

Number of hygrophilous species also increases with time and structure. No hygrophilous species was found at sites without vegetation. At 50 % of the sites with sparse vegetation, 1 hygrophilous species was recorded, but they were missing at the others. Sites with dense vegetation held at least 1 species with a maximum of 6 species both at the littoral site and **sch-ref-2**. The ash-meliorated soil of **sch-den-23** held 4 hygrophilous species. Increase of hygrophilous species is also highly significant ($r = 0.78$, $p < 0.000$).

Eurotopic species are absent at only 2 sites: **Koy-bar-54** and **sch-spa-ref**. At sites without vegetation there was only 1 species at the youngest and the oldest dune. Sites with sparse vegetation held 1 to 3 species. All sites with dense vegetation were colonised by eurotopic species, increasing from 2 species at the youngest site to 5 species at the second oldest reclamation site. **Only at sch-den-29**, just 1 species was found. Their increase with structure is highly significant ($r = 0.72$, $p < 0.001$).

Other species[1] were found at a maximum of 1 species. No other species was recorded from sites without vegetation and younger sites with sparse vegetation. More frequently, at sites with dense vegetation 1 „other“ species occurred (fig.53).

[1] Not classified species here are *Folsomina onychiurina* and *Protophorura meridiatus*. The first was found only at **ple-bar-59**, the latter at **sch-spa-29** and **sch-den-29**.

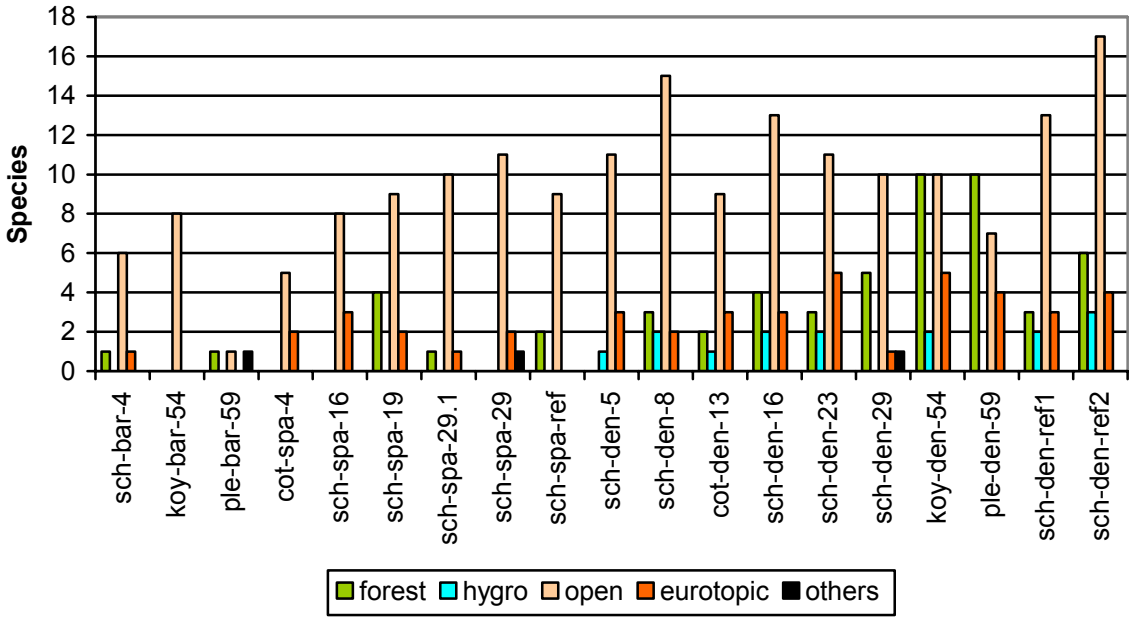


Figure 53: Ecological groups, number of species.

Figure 54: Ecological groups, number of species.

	sch-bar-4	koy-bar-54	ple-bar-59	cot-spa-4	sch-spa-16	sch-spa-19	sch-spa-29.1	sch-spa-29	sch-spa-ref	sch-den-5	sch-den-8	cot-den-13	sch-den-16	sch-den-23	sch-den-29	koy-den-54	ple-den-59	sch-den-ref1	sch-den-ref2
forest	1		1			4	1		2		3	2	4	3	5	10	10	3	6
hygro										1	2	1	2	2		2		2	3
open	6	8	1	5	8	9	10	11	9	11	15	9	13	11	10	10	7	13	17
eurotopic	1			2	3	2	1	2		3	2	3	3	5	1	5	4	3	4
others			1					1							1				
Sum	8	8	3	7	11	15	12	14	11	15	22	15	22	21	17	27	21	21	30

Dominance of ecological groups (species)

Dominance of meadow species decreases with age and structure. At **koy-bar-54**, all species found were typical for open environments. Their dominance decreases from 100.0 % at **koy-bar-54** to 33.3 % at the oldest reclamation site **ple-den-59**. At the reference sites with dense vegetation their dominance increases and they represent 61.9 % to 56.7 % of all species.

Forest species are negatively correlated to species of open habitats. As there was only 1 species found at the youngest reclamation site, the relatively high dominance of 12.5 % is an exception. Generally, forest species are missing the first 20 years but are then found at all older sites except **sch-spa-29.1** and all sites with dense vegetation. They are usually subdominant (7.1 to 12.5) but their dominance increases until they become eudominant at the oldest reclamation sites where there dominance equals that of meadow species. At the reference site with sparse vegetation, forest species are dominant (20.0 %) whereas at the 2 reference sites, they are subdominant (9.1 %) and dominant (15.6 %).

Eurotopic species are dominant at the youngest dune (12.5 %), but again, as only few species were found at the dunes their dominance seems not to be comparable to other sites) and the youngest sites with sparse vegetation (subdominant at **sch-spa-29.1**). However, eurotopic species are missing at the reference site. They are dominant again at most sites with dense vegetation (13.3 % to 20.0 %). They are subdominant only at **sch-den-8** (9.1 %) and **sch-den-29** (5.9 %).

Hygrophilous species are missing in the dunes and sites with sparse vegetation, but are subdominant at most sites with dense vegetation. They are missing only at **sch-den-29** and **ple-den-59**.

Other species occur at **ple-bar-59** (dominant), **sch-spa-29** and **sch-den-29** (both subdominant, fig. 55, tab. 40).

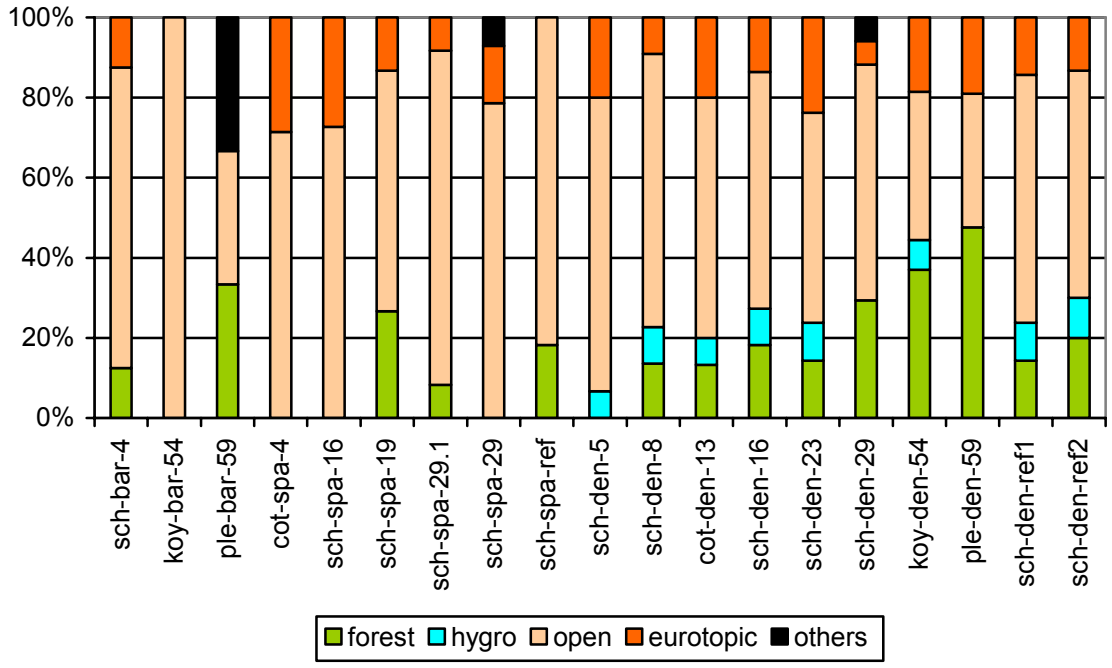


Figure 55: Dominances of ecological groups (species).

Table 40: Dominances of ecological groups (species level), eudominant group marked red.

	sch-bar-4	koy-bar-54	ple-bar-59	cot-spa-4	sch-spa-16	sch-spa-19	sch-spa-29.1	sch-spa-29	sch-spa-ref	sch-den-5	sch-den-8	cot-den-13	sch-den-16	sch-den-23	sch-den-29	koy-den-54	ple-den-59	sch-den-ref1	sch-den-ref2
forest	13	0	33	0	0	27	8	0	18	0	14	13	18	14	29	37	48	14	20
hygro	0	0	0	0	0	0	0	0	0	7	9	7	9	10	0	7	0	10	10
open	75	100	33	71	73	60	83	79	82	73	68	60	59	52	59	37	33	62	57
eurotopic	13	0	0	29	27	13	8	14	0	20	9	20	14	24	6	19	19	14	13
others	0	0	33	0	0	0	0	7	0	0	0	0	0	0	6	0	0	0	0

Specimens per sampling

In absolute numbers per sampling, specimens of meadow species increase with time. At sites with sparse vegetation, their number increases almost constantly from the younger sites to the reference site as “oldest” site. With 85.8 specimens per sampling, the reference site **sch-spa-ref** shows the highest density of meadow specimens. At sites with dense vegetation, number of specimens per sampling varies about 40 to 50 specimens. Exceptions are the ash-meliorated site **sch-den-23** where 74.9 specimens were recorded and the oldest reclamation site **ple-den-59** with only 26.0 specimens. There is no significant correlation to structure ($r = 0.30$, $p < 0.215$).

In sites without dense vegetation, hygrophilous species are absent. They are frequently abundant at sites with dense vegetation and reach a maximum of 5.83 specimens per sampling at the littoral site **sch-den-8**. However, they are missing at **sch-den-29** and **ple-den-59**. Increase of hygrophilous species in highly significant ($r = 0.81$, $p < 0.000$).

Forest species reach their maximum of 33.2 specimens per sampling at the oldest reclamation site **ple-den-59**. They are frequently missing or found only with lowest abundances at sites without dense vegetation. Their increase is significant ($r = 0.61$, $p < 0.006$).

Specimens of eurotopic species reach high numbers in sites with dense vegetation. At **sch-den-8** and the 2 oldest reclamation sites they are the most abundant Collembola. Yet their abundance is rather low at **sch-den-5**, **sch-den-16**, **sch-den-29** and **sch-den-ref1**. Increase of specimens per sampling is highly significant ($r = 0.77$, $p < 0.000$).

Other species are missing in most samples. Their maximum number is 3.29 specimens per sampling at **sch-den-29** (here: *Protaphorura meridiata*, fig. 56).

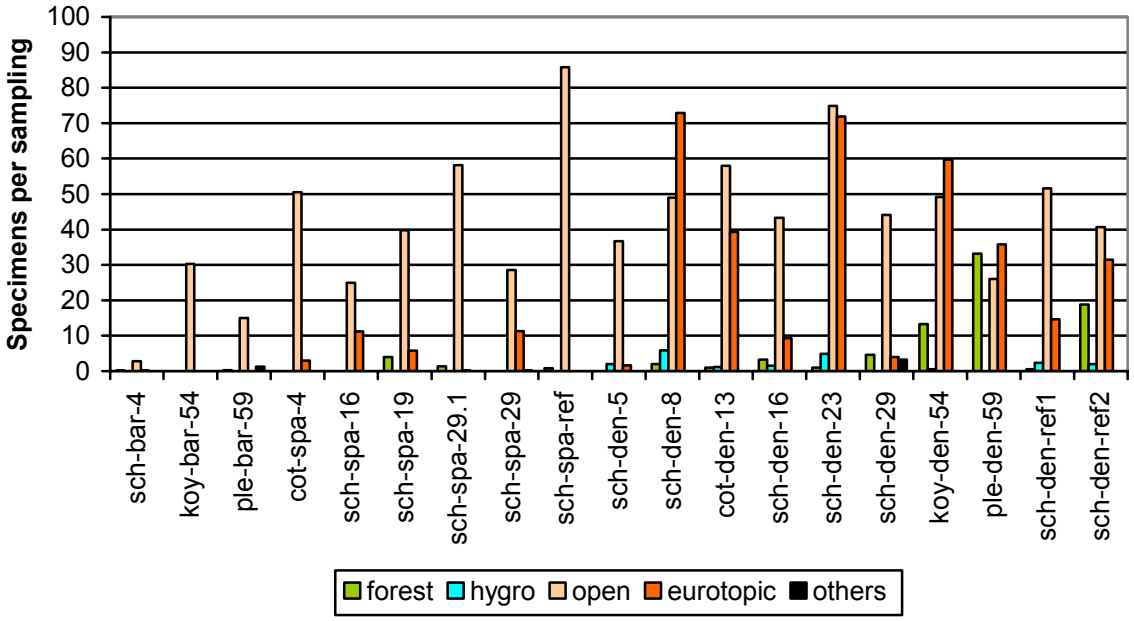


Figure 56: Ecological groups, specimens per sampling.

Dominance of specimens

Meadow species are eudominant at most sites. Dunes and sites with sparse vegetation are dominated by 71.4 % to 100.0 %. Their dominance decreases at sites with dense vegetation but they are still eudominant. At **sch-den-8** and **ple-den-59** they are reduced to dominant species, but still at high levels (37.8 % and 27.4 %). Their decrease in dominance is highly significant ($r = -0.671$, $p < 0.002$).

Eurotopic species have an irregular dominance pattern at dunes and sites with sparse vegetation. They are missing, recedent or even subdominant. At sites with dense vegetation however, they become dominant and even eudominant with the exception of **sch-den-5** (subdominant; 4.1 %) and **sch-den-29** (subdominant; 7.1 %). Their increase in dominance is highly significant ($r = 0.612$, $p < 0.005$)

Forest species are mainly missing, subrecedent or recedent at sites without dense vegetation. Only at **sch-spa-19** they become subdominant[2]. At the oldest reclamation site **ple-den-54** with dense vegetation, they become almost eudominant (34.9 %) and dominant at the 2nd reference site **sch-den-ref2** (14.8 %). An exception is the moss-rich site **sch-spa-19** where they are also subdominant (8.1 %). There is a strong positive correlation to structure which is almost significant ($r = 0.454$, $p < 0.051$).

Hygrophilous species are missing at sites without dense vegetation. They become recedent or subdominant at most sites with dense vegetation. Their increase in dominance is significant ($r = 0.564$, $p < 0.012$).

[2] Again, sch-bar-4 should be looked on critically, as one accidentally drifted specimen becomes automatically subdominant.

Other species (here: *Protaphorura meridiata*) are important as subdominant group at **sch-den-29** (5.9 %). There is no correlation between changes of dominance and structure (fig. 57, tab. 41).

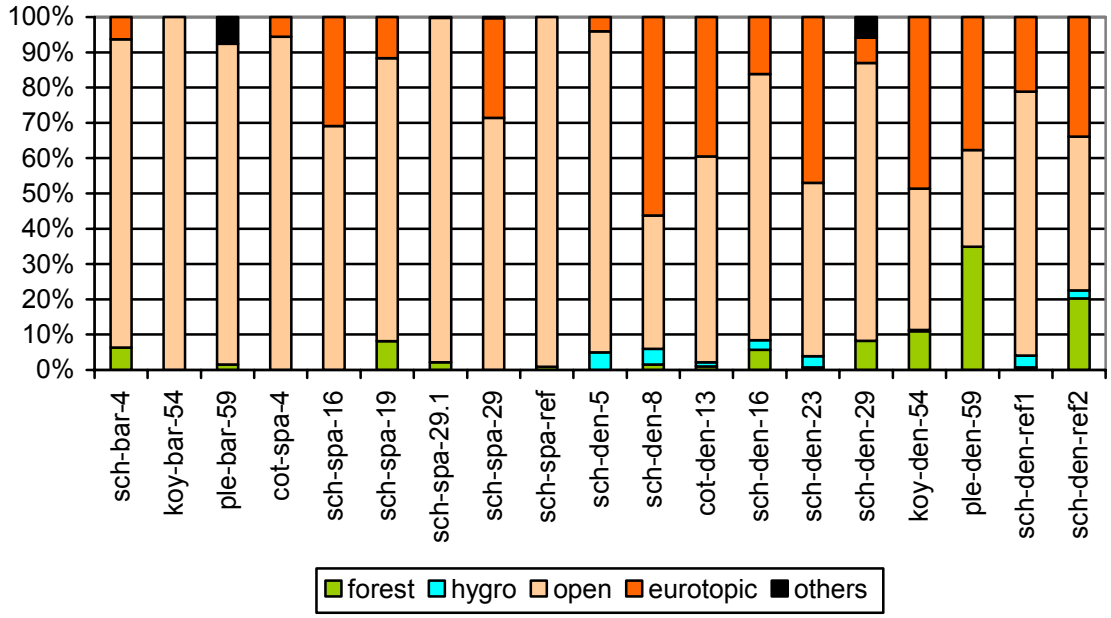


Figure 57: Dominances of ecological groups (specimens).

Table 41: Dominance of ecological groups (level of specimens), eudomanint groups marked red.

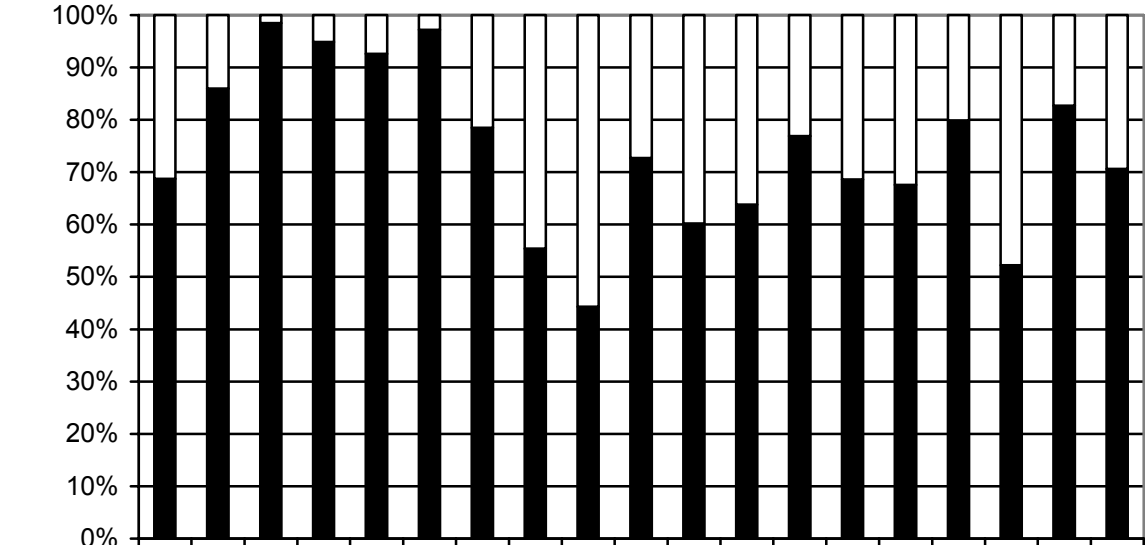
	sch-bar-4	koy-bar-54	ple-bar-59	cot-spa-4	sch-spa-16	sch-spa-19	sch-spa-29.1	sch-spa-29	sch-spa-ref	sch-den-5	sch-den-8	cot-den-13	sch-den-16	sch-den-23	sch-den-29	koy-den-54	ple-den-59	sch-den-ref1	sch-den-ref2
forest	6,3	0,0	1,5	0,0	0,0	8,1	2,2	0,0	0,9	0,0	1,5	1,0	5,7	0,7	8,2	10,9	34,9	0,7	20,3
hygro	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	5,0	4,5	1,2	2,7	3,2	0,0	0,4	0,0	3,4	2,2
open	87,5	100,0	90,9	94,4	69,1	80,2	97,5	71,4	99,1	90,9	37,8	58,3	75,4	49,1	78,8	40,1	27,4	74,7	43,7
eurotopic	6,3	0,0	0,0	5,6	30,9	11,7	0,3	28,2	0,0	4,1	56,2	39,5	16,2	47,1	7,1	48,6	37,7	21,2	33,9
others	0,0	0,0	7,6	0,0	0,0	0,0	0,0	0,4	0,0	0,0	0,0	0,0	0,0	0,0	5,9	0,0	0,0	0,0	0,0

4.2.2.3 Succession of life forms

Specimens: At sites without or with sparse vegetation, euedaphic species are eudominant at highest levels (78.5 % to 98.5 %). They decrease at **sch-spa-29** to 55.4 %. This is most probable a side specific effect as this site is covered to 2/3 by dense vegetation. Epigaeic species are eudominant only at that site and the reference site **sch-spa-ref**.

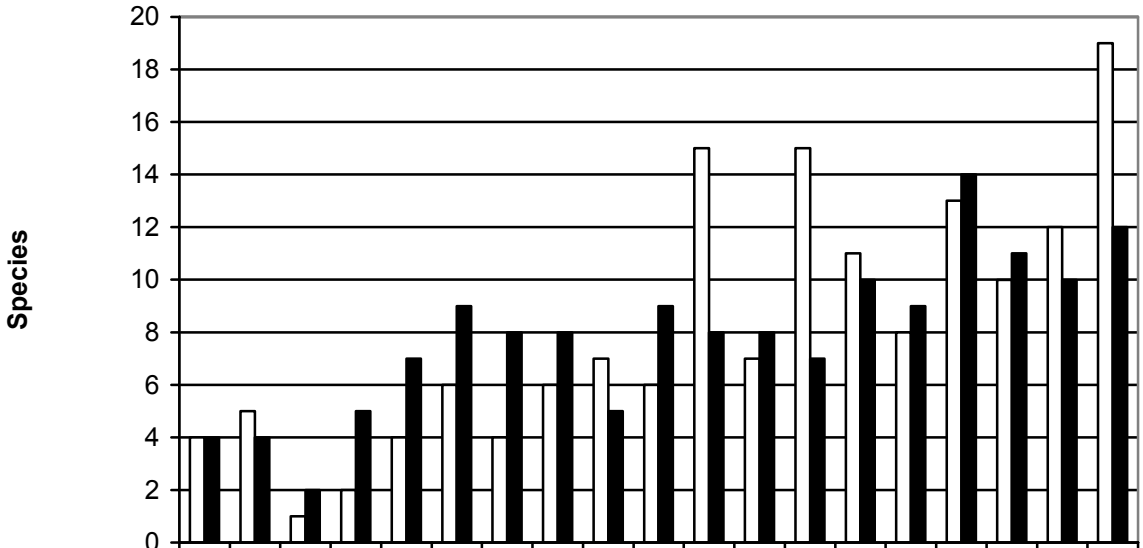
At sites with dense vegetation, dominances vary considerably. Epigaeic species are dominant and even eudominant twice (**sch-den-8; ple-den-59**).

However, changes in dominance on the level of specimens show no significant correlation, neither to structure ($r = 0.084$, $p < 0.732$ for epigaeic and $r = -0.084$, $p < 0.732$ for endogaeic species) nor to age of sites ($r = 0.075$, $p < 0.760$ for epigaeic and $r = -0.075$, $p < 0.760$ for endogaeic species).



	sch-bar-4	koy-bar-54	ple-bar-59	cot-spa-4	sch-spa-16	sch-spa-19	sch-spa-29.1	sch-spa-29	sch-spa-ref	sch-den-5	sch-den-8	cot-den-13	sch-den-16	sch-den-23	sch-den-29	koy-den-54	ple-den-59	sch-den-ref1	sch-den-ref2
epigaeic	31,3	14	1,5	5,1	7,4	2,8	21,5	44,6	55,7	27,3	39,8	36,2	23,1	31,4	32,4	20,1	47,8	17,3	29,4
endogaeic	68,8	86	98,5	94,9	92,6	97,2	78,5	55,4	44,3	72,7	60,2	63,8	76,9	68,6	67,6	79,9	52,2	82,7	70,6

Figure 58: Dominance of life forms, specimens.

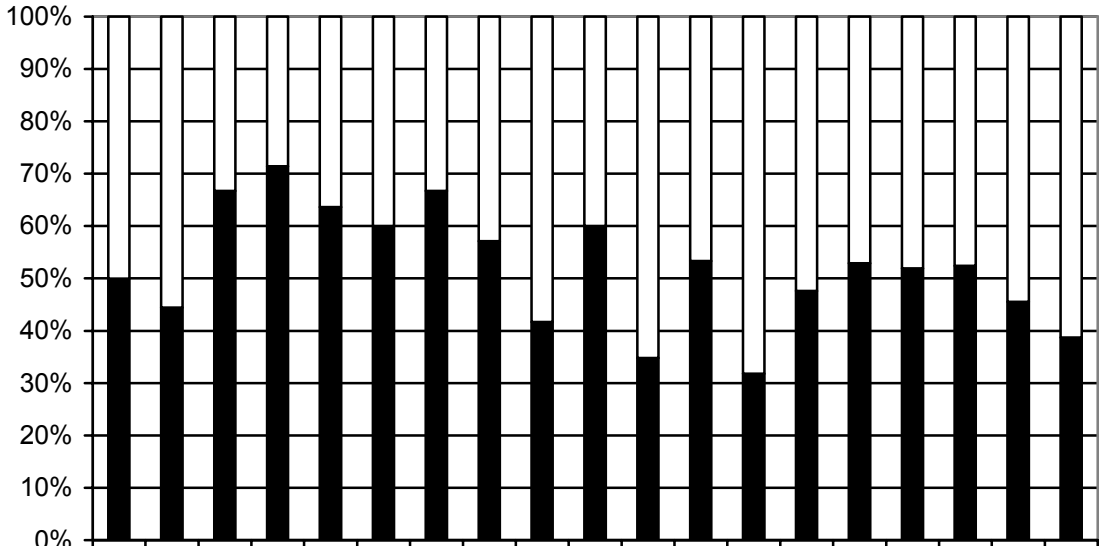


	sch-bar-4	koy-bar-54	ple-bar-59	cot-spa-4	sch-spa-16	sch-spa-19	sch-spa-29.1	sch-spa-29	sch-spa-ref	sch-den-5	sch-den-8	cot-den-13	sch-den-16	sch-den-23	sch-den-29	koy-den-54	ple-den-59	sch-den-ref1	sch-den-ref2
epigaeic	4	5	1	2	4	6	4	6	7	6	15	7	15	11	8	13	10	12	19
endogaeic	4	4	2	5	7	9	8	8	5	9	8	8	7	10	9	14	11	10	12

Figure 59: Species number

Correlation between structure and number of species is highly significantly positive for both life forms ($r = 0.875$, $p < 0.000$ for epigaeic and $r = 0.867$, $p < 0.000$ for endogaeic species). But as shown at the beginning of the chapter, there is no correlation between age of sites and species richness of the different strata ($r = 0.276$, $p < 0.252$ for epigaeic and $r = 0.310$, $p < 0.196$ for endogaeic species).

Endogaeic species dominate the community with 50.0 % to 71.4 % at sites without or sparse vegetation on reclamation sites. At the reference site **sch-spa-ref** more epigaeic than endogaeic species were found. At reclamation sites with dense vegetation, endogaeic species vary between 31.8 % and 53.3 % of dominance (fig. 60).



	sch-bar-4	koy-bar-54	ple-bar-59	cot-spa-4	sch-spa-16	sch-spa-19	sch-spa-29.1	sch-spa-29	sch-spa-ref	sch-den-5	sch-den-8	cot-den-13	sch-den-16	sch-den-23	sch-den-29	koy-den-54	ple-den-59	sch-den-ref1	sch-den-ref2
□ epigaeic	50	55,6	33,3	28,6	36,4	40	33,3	42,9	58,3	40	65,2	46,7	68,2	52,4	47,1	48,1	47,6	54,5	61,3
■ endogaeic	50	44,4	66,7	71,4	63,6	60	66,7	57,1	41,7	60	34,8	53,3	31,8	47,6	52,9	51,9	52,4	45,5	38,7

Figure 60: Dominance of life forms, species level.

There is no correlation between changes in dominance of species and age ($r = 0.262$, $p < 0.278$ for epigaeic and $r = -0.262$, $p < 0.278$ for endogaeic species), but again there is a significant correlation to structure ($r = 0.603$, $p < 0.006$ for epigaeic and $r = -0.603$, $p < 0.006$ for endogaeic species).We find a highly significant positive correlation for epigaeic species and a negative one for endogaeic species.

4.2.2.4 Succession of species

For succession of species, only those species were considered which showed at least some “tendency” or moderate correlation ($p > 0.080 > 0.050$) or significant correlations ($p > 0.050$).

Epigaeic and endogaeic communities were calculated separately as there are obviously different mechanisms working for both communities.

4.2.2.4.1 Succession of epigaeic species

40 species were recorded. All species were tested (Spearman’s Rho) for correlation between changes in dominance and (stand) age.

9 species showed a significant positive correlation to structure (p = 0.050 to 0.000): *Entomobrya multifasciata* ($r = 0.499$, $p < 0.030$), *Isotoma anglicana* ($r = 0.524$, $p < 0.021$), *Isotoma viridis* ($r = 0.652$, $p < 0.003$)*, Lepidocyrtus lanuginosus* ($r = 0.655$, $p < 0.002$), *Lepidocyrtus lignorum* ($r = 0.464$, $p < 0.045$), *Lepidocyrtus*

paradoxus (0.530, p < 0.020), *Sphaeridia pumilis* (r = 0.568, p < 0.011), *Tomocerus flavescens* (r = 0.481, p < 0.037), *Xenylla brevicauda* (r = 0.541, p < 0.017).

1 species showed a tendency (p = 0.080 to 0.050) to be found at sites with more developed vegetation: *Sminthurinus aureus* (r = 0.446, p < 0.055).

30 species showed no significant correlations or tendencies (p = 0.081 to 1.000): *Anurophorus atlanticus* (r = 0.215, p < 0.376)*, Arrhopalites caecus* (r = 0.385, p < 0,104)*, Bourletiella pruinosa* (r = -0.022, p < 0.928)*, Brachystomella parvula* (r = -0.020, p < 0,934)*, Ceratophysella denticulate* (r = 0.086, p < 0.726)*, Ceratophysella succinea* (r = 0.332, p < 0.164)*, Cryptopygus thermophilus* (r = 0.072, p < 0.769)*, Desoria violacea* (r = 0.258, p < 0.286)*, Entomobrya lanuginose* (r = 0.349, p < 0.143)*, Entomobrya marginata* (r = 0.382, p < 0.107)*, Entomobrya multifasciata* (r = 0.499, p < 0.030)*, Entomobrya nivalis* (r = 0.401, p < 0.089)*, Isotomurus palustris* (r = 0.138, p < 0.574)*, Lepidocyrtus cyaneus* (r = 0.185, p < 0.447)*, Micraphorura absoloni* (r = -0.172, p < 0.481)*, Neanura muscorum* (r = 0.260, p < 0.282)*, Orchesella bifasciata* (0.346, p < 0.147)*, Orchesella cincta* (r = 0.258, p < 0.286)*, Orchesella flavescens* (r =0.316, p < 0.188)*, Orchesella villosa* (r = -0.042, p < 0.861)*, , Paratullbergia macdougalli* (r = 0.405, p < 0.086)*, Pseudachorutes subcrassus* (r = 0.301, p < 0.210)*, Pseudoanurophorus alticolus* (r = -0.205, p < 0.400)*, Pseudosinella alba* (r = 0.084, p < 0.733)*, Pseudosinella octopunctata* (r = 0.247, p < 0.308)*, Schoetella ununguiculata* (r = -0.313, p < 0.191)*, Sminthurides malmgreni* (r = 0.344, p < 0.149)*, Sminthurides schoetti* (r = 0.376, p < 0.113)*, Sminthurus nigromaculatus* (r = 0.174, p < 0.475)*, Sminthurus viridis* (r = 0.344, p < 0.149)*, Tomocerus vulgaris* (r = -0.094, p < 0.702)*.*

Development of moderately and significantly correlated species, which are at least subdominant in one site, is studied in more detail.

Changes in dominance of selected species

For the purpose of clarity, the figure for 9 species was divided into three single figures.

Entomobrya multifasciata is generally missing at sites with bare soil or sparse vegetation. Exceptions are **koy-bar-54**, were it is a subdominant species (5.3 %). At **sch-spa-29.1** and **sch-spa-29** the species is dominant (15.6 % and 17.6 %). Both sites are distinguished from the other spa-sites: The first is covered to 2/3 by dense vegetation and the second one is covered by moss. At sites with dense vegetation it is missing at the littoral site **sch-den-8** and **sch-den-ref1** and recedent at **ple-den-59** (2.2 %). At the other sites with dense vegetation it is at least subdominant and dominant. At **cot-den-13** it is even eudominant (fig. 61).

Isotoma anglicana is generally missing at dunes and the youngest site with sparse vegetation. At **sch-bar-4** it is dominant (20.0 %), but again this might be due to very low abundances. It is generally a subdominant (6.3 %) to dominant (26.4 %) species at sites with sparse vegetation, but missing at the youngest reclamation site and the reference site **sch-spa-ref**. At sites with dense vegetation its dominances vary strongly from missing at **sch-den-5** and **sch-den-16** to eudominance at **sch-den-23** (48.4 %). At the reference sites it is only subdominant (8.3 %) and subrecedent (1.2

%). The strong variance is probably due to site specific effects which will have to be discussed later (fig. 61).

Isotoma viridis appears only at sites with dense vegetation. At the younger sites it is subrecedent and only at the oldest reclamation sites it becomes subdominant (11.5 % and 6.2 %) same as at **sch-den-ref2** (11.4 %; fig 61).

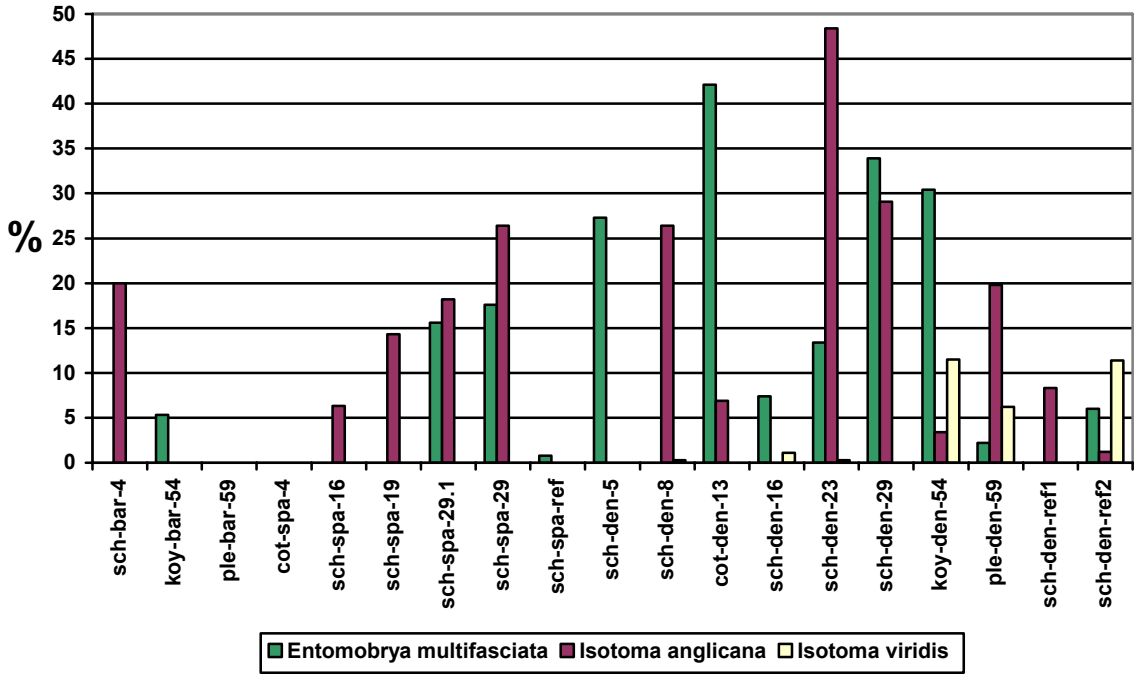


Figure 61: Epigaeic species with significant positive correlations or strong positive tendencies to struture, only species which are at least subdominant once.

Lepidocyrtus lanuginosus appears first as subrecedent species (0.6 %) at the littoral site **sch-den-8**. It is dominant at **sch-den-16** (17.9 %), but missing at **sch-den-23** and recedent at **sch-den-29**. At the two oldest reclamation sites it is subdominant (6.8 % and 9.3 %) same as at **sch-den-ref2** (6.6 %; fig. 62).

L. lignorum was the only epigaeic species at **ple-bar-59** with one single specimen and is therefore automatically eudominant with 100 %. Neglecting this site for obvious reasons, the species appears first at **sch-den-16** as subdominant (4.2 %) and then again at the two oldest reclamation sites as dominant species (21.6 % and 33.9 %) same as at **sch-den-ref2** (31.9 %; fig. 62).

L. paradoxus was found only at the reference sites **sch-den-ref1** where it is eudominant (41.7 %) and **sch-den-ref2** where it is but subrecedent (0.6 %). Both sites are mainly distinguished by moisture (fig. 62).

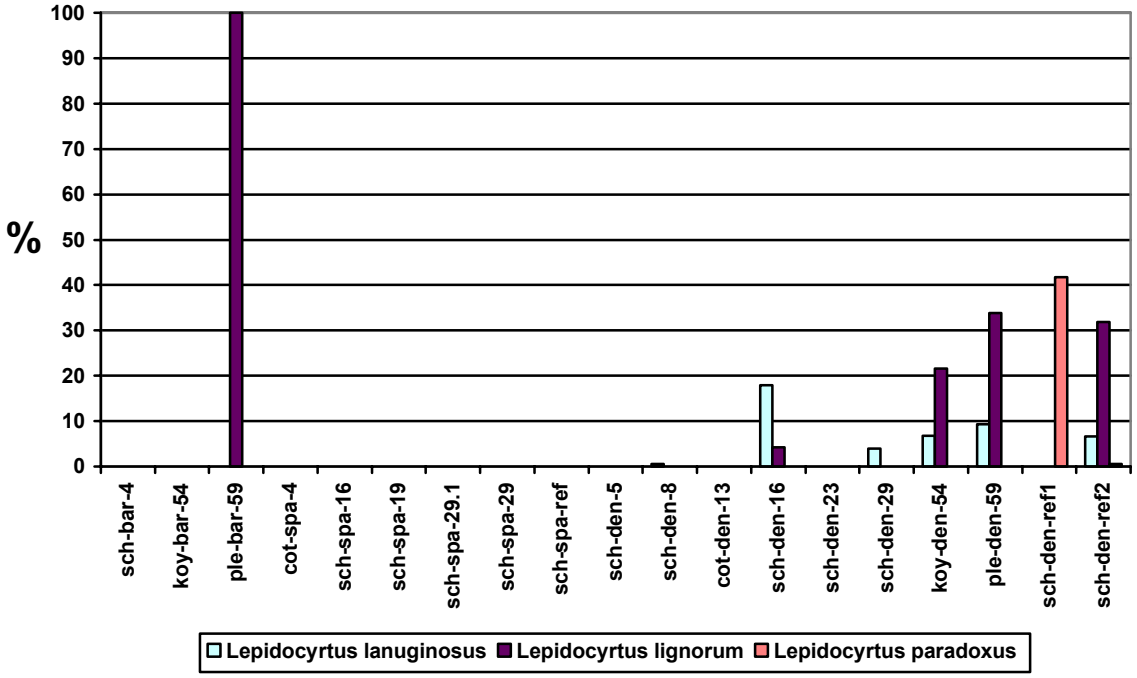


Figure 62: Epigaeic species with significant positive correlations or strong positive tendencies to struture, only species which are at least subdominant once.

Sphaeridia pumilis was never found at dunes or sites with sparse vegetation. At **sch-den-5** it is dominant (18.2 %) same as at the reference site **sch-den-ref1** (18.1 %). It is subdominant at **sch-den-8** (10.6 %), **sch-den-16** (10.5 %) and **sch-den-23** (6.9 %). At **sch-den-13** (3.2 %), **koy-den-54** (1.4 %) and **sch-den-ref2** (3.0 %) it is recedent. The species is missing at **sch-den-29** and **ple-den-59** (fig. 63).

Tomocerus flavescens was only found at sites with dense vegetation. It is subrecedent at **sch-den-16** (1.1 %), subdominant at **koy-den-54** (6.8 %) and recedent at **sch-den-ref2** (1.8 %; fig.63).

Sminthurinus aureus was found with a single specimen each at **koy-bar-54** (5.3 %) and **sch-spa-16** (6.3 %) as subdominant species. It appears more frequently at sites with dense vegetation where it is recedent at **sch-den-5** (1.5 %), **koy-den-54** (1.4 %) and **sch-den-ref1** (2.8 %) and subrecedent at **sch-den-8** (0.6 %). It is subdominant again at **sch-den-16** (9.5 %) and **sch-den-ref2** (9.6 %) and only dominant at **sch-den-23** (14.6 %; fig.63).

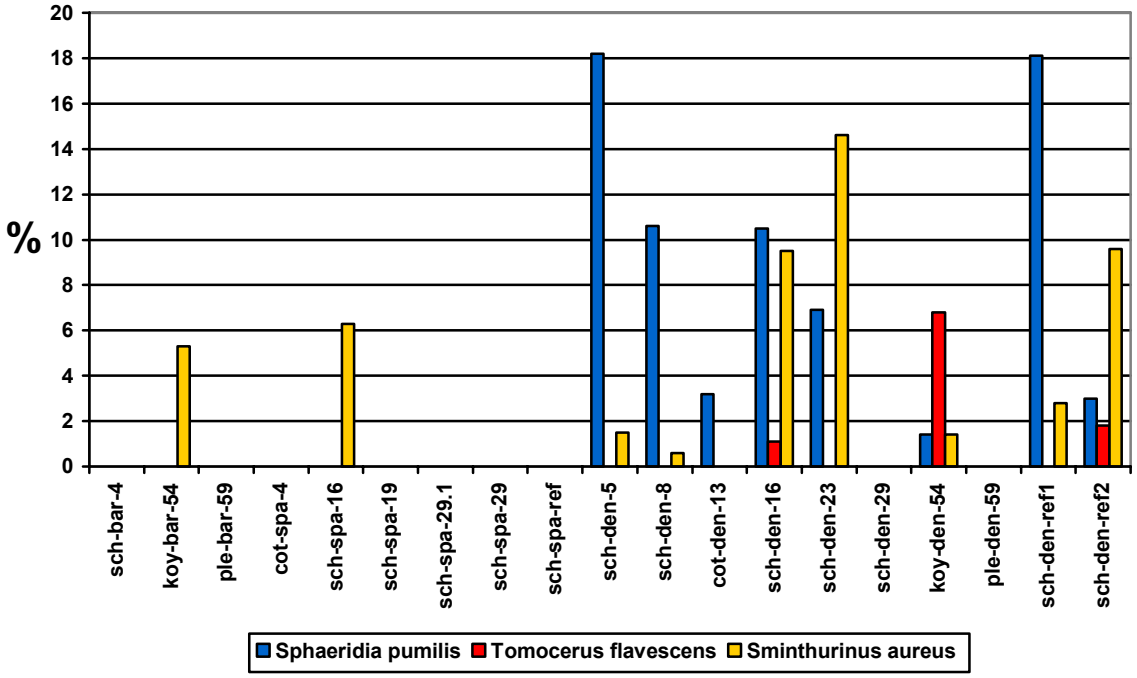


Figure 63: Epigaeic species with significant positive correlations or strong positive tendencies to struture, only species which are at least subdominant once.

4.2.2.4.2 Succession of endogaeic species

32 species were recorded. All species were tested (Spearman's Rho) for correlation between changes in dominance and age.

3 species showed a significant positive correlation to structure: *Folsomia candida* (r = 0.612, p < 0.005), *Folsomia fimetaria* (r = 0.620, p < 0.005), *Parisotoma notabilis* (r = 0.741, p < 0.000),

1 species showed a significant negative correlation to structure (p = 0.050 to 0.000): *Mesaphorura atlantica* (r = -0.538, p < 0.017).

1 species showed a tendency (p = 0.080 to 0.050) to be found at sites with more developed vegetation: *Friesea mirabilis* (r = 0.503, p < 0.028).

27 species showed no such tendencies or significant correlations: *Cyphoderus albinus* (r = 0.408, p < 0.083), *Folsomia dovrensis* (r = 0.301, p < 0.210), *Folsomia manolachei* (r = -0.215, p < 0.376), *Folsomia onychiurina* (r = -0.301, p < 0.210), *Folsomia penicula* (r = 286, p < 0.235), *Heteromurus nitidus* (r = 0.258, p < 0.286), *Hypogastrura manubrialis* (r = 0.172, p < 0.481), *Isotomiella minor* (r = 0.389 p < 0.100), *Isotomodes productus* (r = 0.381, p < 0.107), *Mesaphorura critica* (r = -0.013, p < 0.957), *Mesaphorura hylophila* (r = 0.256, p < 0.290), *Mesaphorura italica* (r = 0.344, p < 0.149), *Mesaphorura krausbaueri* (r = 0.355, p < 0.135), *Mesaphorura macrochaeta* (r = 0.179,p < 0.464), *Mesaphorura tenuisensillata* (r = 0.000, p < 1.000), *Metaphorura affinis* (r = 0.215, p < 0.376), *Micranurida pygmea* (r = 0.002, p < 0.994), *Microanurophorus musci* (r = 0.190, p < 0.425), *Proisotoma minima* (r =

0.240, p < 0.322), *Proisotoma minuta* (r = 0.034, p < 0.891), *Protaphorura armata* (r = 0.322, p < 0.179), *Protaphorura meridiata* (r = 0.105, p < 0.668), *Seira domestica* (r = 0.339, p < 0.156), *Vertagopus arboreus* (r = 0.378, p < 0.110), *Willemia anophthalma* (r = 0.197, p < 0.418), *Willemia aspinata* (r = -0.172, p < 0.481), *Willemia intermedia* (r = -0.002, p < 0.993).

Development of moderately and significantly correlated species, which are at least subdominant in one site, is studied in more detail.

Changes in dominance of selected species

Folsomia candida was never found at sites without dense vegetation. Even there, it becomes subdominant just once at **koy-den-54**. It is subrecedent at **cot-den-13** (0.3 %) and recedent at **ple-den-59**. At the drier reference site **sch-den-ref1** it is subdominant again (9.0 %; fig. 64).

Friesea mirabilis was just once found at the oldest reclamation site **ple-den-59** as subrecedent species (1.2 %). At the wetter reference site **sch-den-ref2** it is subdominant (7.4 %; fig. 64).

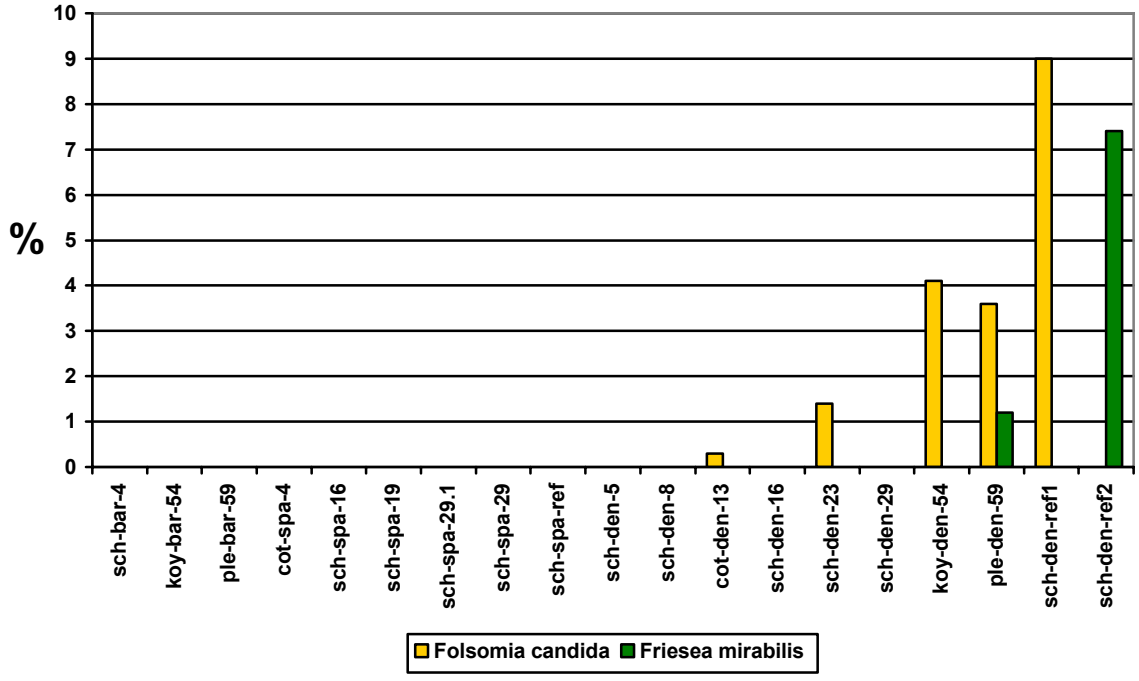


Figure 64: Endogaeic species with significant positive correlations or strong positive tendencies to struture, only species which are at least subdominant once.

Mesaphorura atlantica is only eudominant at sites without dense vegetation: **sch-bar-4** (54.5 %), **ple-bar-59** (92.3 %) and **sch-spa-29.1** (82.6 %). It is subdominant at other sites (**koy-bar-54** 5.9%, **cot-spa-4** 7.9 %, **sch-spa-19** %) but missing at **sch-**

spa-16. At sites with dense vegetation, the species is missing or subrecedent. Only at **sch-den-ref1** it is subdominant (7.0 %; fig. 65).

Parisotoma notabilis is generally recedent, subrecedent or missing at sites without dense vegetation. Only **at sch-bar-4** the single specimen found becomes subdominant (9.1 %). At sites with dense vegetation, the species is subdominant and dominant but generally eudominant (**sch-den-8** 82.2 %, **cot-den-13** 60.9 %, **sch-den-23** 52.0 %, **koy-den-54** 53.4 %, **ple-den-59** 66.9 %). Only at the youngest reclamation site with dense vegetation, **sch-den-5**, it is recedent (2.3 %; fig. 65).

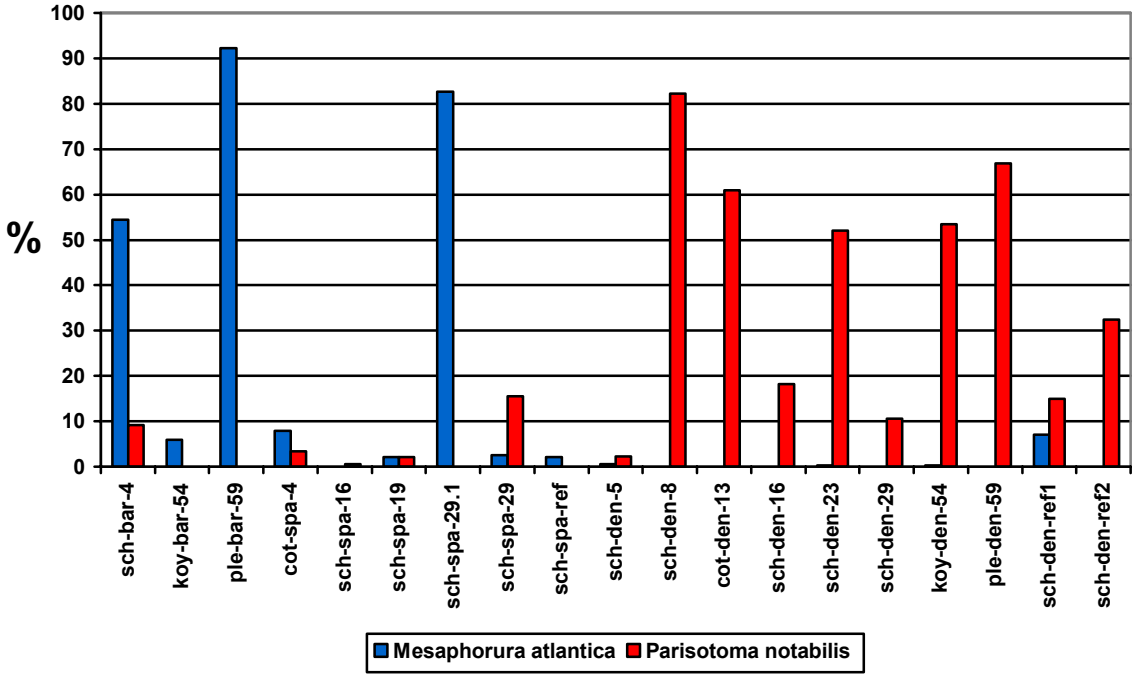


Figure 65: Endogaeic species with significant correlations or strong tendencies to struture, only species which are at least subdominant once.

4.2.2.5 Cluster analysis

Cluster analysis distinguishes 3 main groups. The first group contains 7 sites with dense vegetation. This group of sites is characterised by a *Parisotoma notabilis* community. The 2nd main group consists of sites with sparse vegetation and without vegetation and is further divided into 2 subgroups. The first subgroup of 3 sites contains sites with *Mesaphorura atlantica* dominance and **sch-spa-29.1** which is *Proisotoma minuta* dominated. The 3rd main group of 8 sites is dominated by a *Mesaphorura macrochaeta* community. All tree types of structure are represented, but of dense vegetation there are generally younger sites. Again, the edaphic community explains the cluster tree (fig. 66).

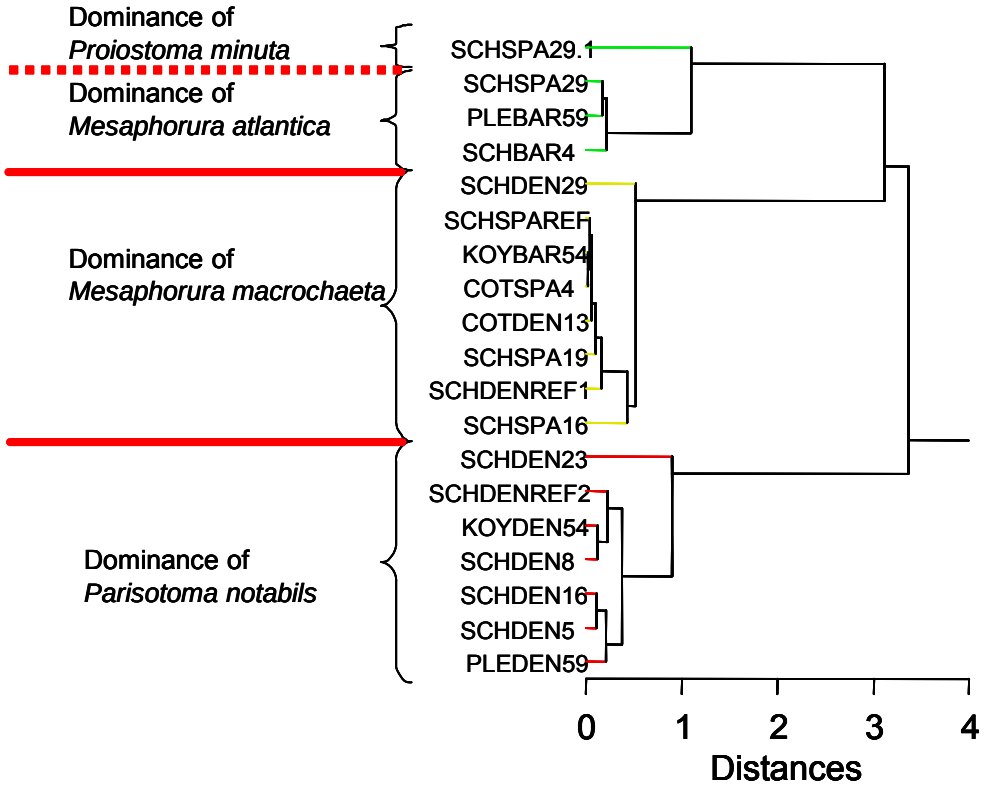


Figure 66: Cluster analysis of Collembolan communities of sites with free succession (Distance metric is 1-Pearson correlation coefficient, Ward minimum variance method).

Table 42: Distance metric is 1-Pearson correlation coefficient, Ward minimum variance method.

Cluster containing	And cluster containing	Were joined at distance	No. of members in new cluster
COTSPA4	KOYBAR54	0.020	2
SCHSPAREF	COTSPA4	0.037	3
COTDEN13	SCHSPAREF	0.053	4
SCHSPA19	COTDEN13	0.095	5
SCHDEN16	SCHDEN5	0.110	2
KOYDEN54	SCHDEN8	0.113	2
SCHDENREF1	SCHSPA85	0.155	6
SCHSPA29	PLEBAR59	0.165	2
PLEDEN59	SCHDEN16	0.206	3
SCHSPA29	SCHBAR4	0.217	3
KOYDEN54	SCHDENREF2	0.228	3
PLEDEN59	KOYDEN54	0.376	6
SCHSPA16	SCHDENREF1	0.421	7
SCHSPA16	SCHDEN29	0.514	8
PLEDEN59	SCHDEN23	0.898	7
SCHSPA29	SCHSPA291	1.097	4
SCHSPA16	SCHSPA29	3.117	12
PLEDEN59	SCHSPA16	3.367	19

5. Discussion

5.1 Methods

There are several critical questions to be asked which are concerning the methods. Most of all, the choice of **study sites** and **sampling design** was less than optimal for soil ecological studies.

Chronosequences are only suboptimal whereas longtime studies on the same area much more reliable. Such studies are few and mainly the works of DUNGER (1968, 1975, 1979, 1984, 1991, 1994, 1998, 1999, 2001) are based on real-time studies and therefore more reliable as they are not afflicted with the following problems:

- Care has to be taken to find sites of similar site properties, but even with great care, variation exists and not all assumptions for similarity will meet in the end.
- There is an ordering of these sites according to *a priori* ideas how succession proceeds. But pathways of succession are still in discussion (SCHREIBER 1997, DUNGER & WANNER 1999, FELINKS 2000).
- It is assumed that the faunal communities are intrinsically related in structure to the surface vegetation, and that boundaries used to define plant communities can be meaningfully used to delimit animal communities. But homogeneity of surface vegetation does not *per se* preclude heterogeneity of faunal communities (PARR 1978).

These problems are inherent in the chronosequence approach and have been recognized previously in ecosystem processes and biodiversity studies (PARR 1978, COLE & VAN MIEGROET 1989, KREMSATER & BUNNEL 1998).

When the study sites where chosen, no soil ecologist was invited to take part in the discussion. Focus was on epigaeic arthropods and small mammals. Therefore, this work has to compare extreme sandy soils (**sch-spa-ref**) with lime containing soils (**sch-den-ref**) and ash-meliorated soils (**sch-den-23**); lake shores (**sch-den-8**) with dry dunes (**ple-spa-54**); young meliorated sites with high pH (**cot-spa-4**) with young unmeliorated ones with low pH (**sch-bar-4**). So there was a real problem in arranging sites within the chronosequence of the successional sites. However, the used structural chronosequence delivered useful and reliable results if we compare literature: LIIRI et al. (2002) found that species richness of microarthropods was lower in ash-treated sites than in control plots although this was mainly due to a decrease of oribatid mites. SHAW (2003) studied Collembola of pulverised fuel ash sites, substrate that is comparable to the ash used for melioration in the PML. He states that during the weathering process a succession akin to that of sand dunes takes place and we may therefore be optimistic that the results match with those from the sandy sites although ash and sand are per se not comparable.

Outliers, which are due to different melioration praxis, extreme moisture or other soil conditions in certain sites can be spotted and kept in mind when discussing the results. Moreover, these special sites provided some species (e. g. *Seira domestica, Hypogastrura manubrialis*) and communities that were not found on any other sites.

The results from some sites like **ple-bar-59** suffered from surrounding side effects. A small dune within woodland is supposed to contain forest species in its samples and indeed, 1/3 of its entire species were forest species. This site provided only very few specimens, so the accidentally found forest species makes interpretation of such sites quite hard or even impossible.

An unexpected bias was due to the activities of wild boars. The pitfall-traps used for epigaeic arthropods were filled with ethylenglycol which attracted wild boars. In their attempt to get at the ethylenglycol the soil around some sampling sites was disturbed. Particularly **sch-pin-88** A and B were regularly affected by this disturbance.

The standardised method for calculating organic matter content is loss on ignition in percent. This method has its deficiencies in the PML as the dumped soils still contain different amounts of lignite in form from dust to quite large pieces of lignite (fig. 67).

Figure 67: Examples for different amounts of coal at Plessa, Schwarzer Berg (March 2004) and at a reclaimed agricultural area at the PML Jänschwalde (May 2004). A one-cent coin was used to show the proportions of the remaining lignite.

Therefore, one cannot distinguish between incinerated new accumulated humus and incinerated remains of lignite. According to the method, strongly lime containing soils can also add to the bias for loss on ignition, as in those soils not only organic matter is ignited but also the containing lime. But this is for example probably the case with reference site **sch-den-ref2**.

It is generally agreed, that most reclamation sites are most heterogeneous in their soil parameters due to the conveyor belt technology (HARRANDINE 1949, SCHAFER 1979, WILDING & DREES 1983, KEPLIN & HÜTTL 2000). Exceptions are sites carefully meliorated for agriculture (**sch-den-23**), which seem to be more homogenous than undisturbed, natural sites. Detailed knowledge of geological substrate as well as type of equipment used in mining is a prerequisite for comparisons of faunal succession at strip mine dumps. Older spoils in the Lusatian mining area were dumped using rather primitive techniques. More demanding reclamation technologies are generally demanded since 1980 by the Federal Mining Act which claims a “bed of arable land” to the depth of 0.6 to 1.0 metres of topsoil (DUNGER ET AL. 2001). Therefore, it was quite optimistic to believe that the chosen sampling design would reflect the changes in soil parameters for all sites sufficiently. Soil arthropods react very sensitive within few centimetres on heavy changes in soil parameters (**sch-spa-29**, **sch-den-8**). Transect sampling by the author at the end of the study proved this fact (unpublished data). Therefore, transects should be the method of choice in these heterogeneous

sites. Moreover, each soil sample should be studied for pH, organic matter content, water content and water capacity. Ecological studies, which aim at the food web, should start the sampling designs with the smallest unit of interest and develop the sampling design further. Here, it was the other way round and the data for Collembola got some unnecessary fuzziness.

Another critically viewed point is the fact, that the forest chronosequence deals with exotic plants (*Quercus rubra, Pinus nigra*) on the reclamation sites, but compares them to *Quercus petraea* stands as reference sites. The differences found can be due to reclamation techniques like melioration or due to different forest communities. For example, poor developed soil fauna was found by DUNGER et al. (1997) at Domsdorf at an ash-meliorated site which had been afforested with *Quercus rubra* some 35 years before. They ascribe it to the exotic oaks and "bad ecological restoration". So the choice of study sites in this work was far less than optimal. In connection with the exotic tree afforestation such as *Quercus rubra* or *Pinus nigra,* KOVÁC et al. (2004) hint at the fact that there is a rupture of Collembola community structure and dynamics in exotic monocultures. But generally, coniferous woodlands do not exhibit profound changes in collembolan communities when compared to deciduous woodlands, but forest influence is at a maximum at deciduous forests (PONGE et al. 2003), so results would generally be comparable.

Acidic afforested mine-soils show slower succession than non-acidic soils (DUNGER 1991). Pyrite-rich Lower Lusatian dump soils bore only a weak developed soil arthropod community as have dumps surrounded or afforested with *Pinus* (DUNGER 1989, WANNER & DUNGER 2002). Coniferous forest soils contain less moisture than that of comparable beech forest soils (CASSAGNE et al. 2004). However, a 35 years old red oak afforestation at Domsdorf showed a weak species composition of only 14 species compared to a pine afforestation of the same age at Domsdorf with 25 species (DUNGER 1997). Mixed afforestations with red oak and lime-trees on an ash-meliorated site at Domsdorf showed very low abundance of Collembola. A litter layer was largely missing. Abundance was about 1/7 fewer than at of an also studied pine-afforestation at Domsdorf (DUNGER 1997). At **dom-pin-37** in this work, only 14 species could be found. Collembola communities are the same under oaks and pines as long as the type of humus is the same (PONGE 1993). Communities of Collembola in different soils at the same location are fairly uniform (ROCHEFORT ET AL. 2006, BUTCHER ET AL. 1971). These results are all strongly contradicting and indicate the urgent need for more detailed studies.

The general conclusion must be to take much more care in choosing the study sites and of course to include a soil ecologist in the process of choosing these sites!

Sampling itself also needs to be discussed. Some purists argue that soil ecological studies should take care not to destroy the soil cores and the pore volume. It is supposed that Collembola cannot be extracted from the soil sample sufficiently, if the pore system is disturbed. This might be the case in highly compact soils like clay where soil pores can be smeared easily. The author has experienced such difficulties in former studies. But soil in the PML mainly consists of sandy soils of different textures. Especially during dry periods, it was impossible to extract a soil core rather than some defined volume of loose sand from the ground. The technically and financially expensive MacFayden-device could therefore not perform its advantages like preserving the soil texture. As the less expensive Berlese-Tullgren-funnels can deal with such loose samples (SCHULZ, pers. comment), the author would use them for future studies instead of the more complex MacFayden-devices.

Another advantage generally connected to MacFayden-devices is the possibility to control temperatures. The samples are heated from above and cooled from below; the heating can be controlled by a thermostat. Some devices use water for cooling, others like the one in this study, use cool air from a refrigerator. Within this study, the general gradient of temperatures was about 15°C after temperature was gradually increased to 40°C. This is a generally accepted method (e. g. PARSONS & PARKINSON 1986, STERZYNSKA, M. & EHRNSBERGER, R. 2000) to avoid quickened drying of the samples. PETERSEN (1978) studied extraction efficiencies in high gradient devices and indicated values between 80% and 90% for Collembola. Besides, differences between Collembola species were demonstrated. As HAGVAR (1982) points out, an optimal heating may vary with the physical and thermal properties of the soil, and also with the microclimate to which the animals are adapted. But samples from the PML are generally already rather dry (compare water content, chapter 5). Soil temperature in the PML can vary considerably. FELINKS (2000) shows in a diagram the variety of soil temperature for the study site **ple-pin-20** (study site 413 in her work) in May 1997. Temperature varied from 0°C to about 58°C within ten days, and 14°C to 58°C within a single day. In the PML we mainly deal with xerothermic sites and species. They are well adapted to heat and drought. It can be doubted that this standard method is the most optimal method for these sites. If one deals with samples from mesic sites like natural forests or wetlands, than the MacFayden may be the suitable method at hand with possibilities to adjust temperature carefully. But for the needs of PML-soils, simple Berlese-Tullgren-funnels will be sufficient.

Statistic is a very useful tool for showing correlations which are not obviously presenting themselves or to put one's data on a mathematically sure basis. However, even significant correlations do not necessarily have to be real correlations beyond their mathematical data base. We all know of the example from HOFER et al. (2004) of the increase of stork populations in Lower Saxony and the increase in home births in this area. Only very romantic souls will take this correlation for real that more storks to deliver babies result in more babies being born at home. Their article was written as "… an example of how studies based on popular belief and unsubstantiated theory, seconded by low quality references and supported by coincidental statistical association could lead to apparent scientific endorsement" (HOFER et al. 2004: 88). So statistic is a very useful tool, but should be used carefully as all tools.

So, various errors are connected with the present data. However, HAGVAR (1982) already explained that if there is a standardization of the methods, then the material should allow for general comparison between habitats and species.

Finally, there is a very basic point to make. It seems impossible in Germany for scientists to concentrate on their work. One is paid only halftime, but not only supposed to work on the study fulltime (regardless if payment is sufficient after all the expanses and debts made as student), present endless publications, represent the university and the project at several symposia and congresses but also support lecturing and administration at university. How these working conditions shall result in quick PHD theses no one knows.

5.2 Soil parameters

Figure 69 shows correlations between soil parameters. Most parameters are significantly correlated to each other. Only **phosphate** shows no correlations or even tendencies to any other parameter. If phosphate is not correlated to (vegetation) structure, than it can be concluded that it is not a limiting factor for plant growth in the PML. Besides, only 4 Collembola species are significantly correlated to phosphate. These species are generally ubiquists like *Folsomia candida* and *Parisotoma notabilis*. As ecological group (species level), eurotopic species are significantly correlated to phosphate.

Nitrate however is significantly positively correlated to structure. Sites which are dominated by *Calamagrostis epigejos* indicate better nutrition (JAKOB et al.1996). The development of plant cover with the consequent development of a litter layer is the key process for the colonisation of soil fauna (SHAW 2003). Collembola communities reflect the development of vegetation (SLAWSKA 1997). This does not necessarily include a diverse plant community, but a certain vegetation structure (ROCHEFORT et al. 2006). So nitrate obviously influences plant growth and the accumulation of organic matter. With the accumulation of humus also water capacity and water content are positively influenced. It results in high microbial activities and therefore is correlated with ammonium as indirect indicator for microbial activity. 6 species are significantly correlated to nitrate; they are mainly ubiquists and forest species. PINTO et al. (1997) stressed the importance of nitrogen content influencing the densities and structure of the collembolan communities. Content of nitrogen controls palatability of the leaves to soil fauna and supports higher fungal biomass (WALLWORK 1976, PETERSEN & LUXTON 1982, PONGE 1999).

Ammonium is significantly correlated to a great number of species. Most of these 21 species are again forest species and ubiquists. Hygrophilous species are also significantly positively correlated to ammonium. They most certainly benefit from microbial activity.

The role of **conductivity** cannot be found by the species significantly *positively* correlated as there are none. But 3 species are significantly negatively correlated to conductivity. These 3 species are indicators for the poorest sites in this study. So we may conclude that conductivity might be a measure to proof soil richness as far as Collembola are concerned.

SLAWSKA (1997) speculates that **soil-moisture** of micro-habitats can be a base factor for development of Collembolan community. Water content and water capacity are quite similarly correlated to certain species. However, water capacity is correlated to some more species (19 species to capacity; 15 species to content). Although the same species are dealt with, the significancies for water capacity are generally higher than for water content. Water content is always just a parameter of a certain moment in time, whereas water capacity does hardly vary. Moreover, water capacity is also an indicator for pore volume. Therefore, water capacity might be a more interesting parameter for future researches. Soil moisture characteristics improve with the development of vegetation (SLAWSKA 1997). But also humus accumulation influences water content and capacity. Forest and hygrophilous species are generally significantly positively correlated to both parameters. Spoil moisture and temperature extremes rather than spoil pH influence composition and spatial distribution of most collembolan populations (PARSONS & PARKINSON 1986). Species richness of total

Collembola and of sucking feeders correlated positively with the water content of the organic layer (HASEGAWA et al. in press).

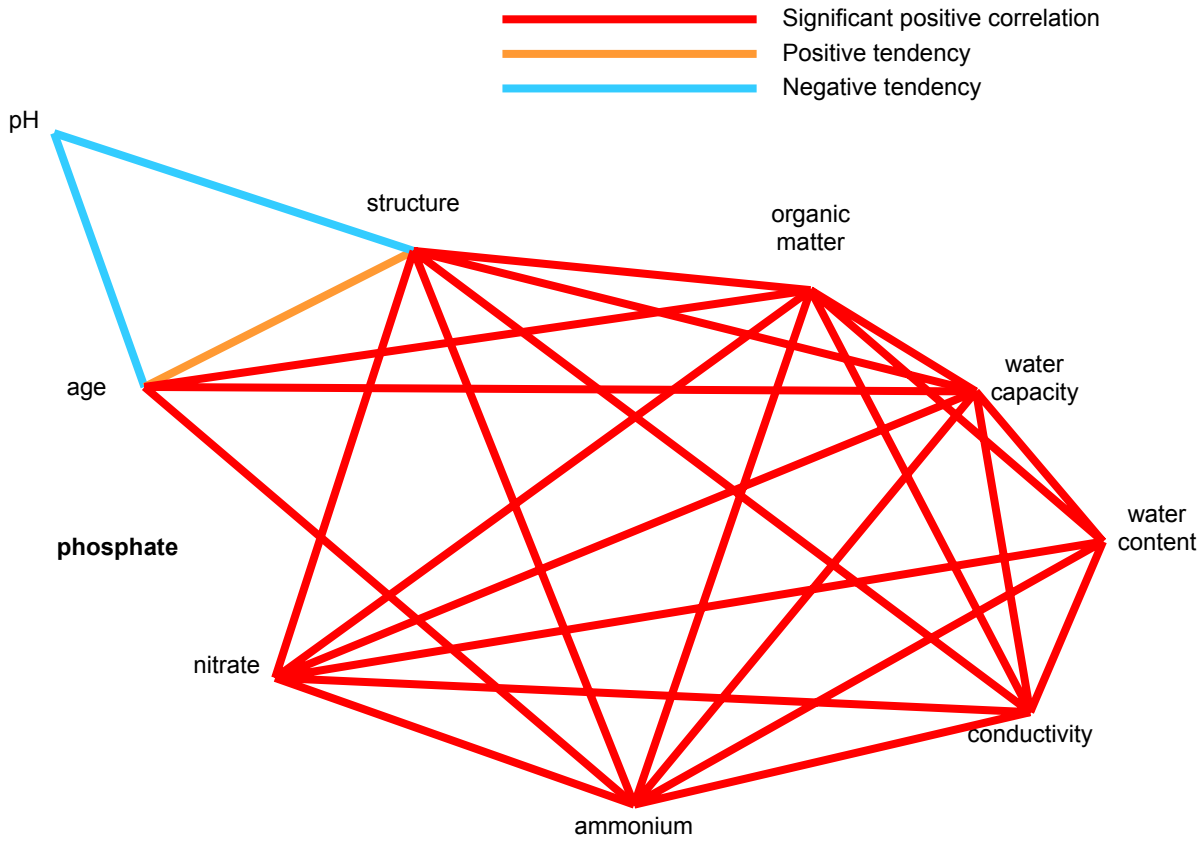


Figure 68: Correlation diamond of soil parameters.

Organic matter content increases with age and is depending on parameters influencing plant growth and thus on structure and age of sites (SHAW 2003). As already mentioned, it also influences water content and capacity and microbial activities (ammonium). 18 species (mainly forest species) are significantly positively correlated to organic matter content. Forest species are generally significantly positively correlated to organic matter content. But again there are the same 3 species negatively correlated as was mentioned for conductivity. CASSAGNE et al. (2003) found that Collembola in forest soils seem to be linked closer to the physical structure of humus than to its chemical parameters.

It is interesting to note that a number of Collembola species follow vegetation structure, hence the number of plant species, with rather low values in the “youngest” sites and an increase in the older sites. This observation is similar to HAGVAR (1982) who concludes a connection between litter consisting of the remnants from a large number of plant species and a greater number of niches for Collembola. Changes in soil texture, chemistry and microflora may also be of importance. Of the 18 species significantly positively correlated to structure are almost exclusively forest species. Forest species are generally significantly positively correlated to structure. One species is significantly negatively correlated. Structure is correlated to all parameters and the correlation is significantly positively but for age and pH. Structurally more

developed sites in this work are mainly dense Calamagrostis stands. At sites with dense *Calamagrostis epigejos* vegetation, 62 % of the coverage may be to litter (JAKOB et al. 1996) and therefore an important habitat for epigaeic species.

In contrast, age of sites lacks the correlation to nitrate. To structure there is no significant correlation as we already know that there is no strict chronological succession in the PML. Even after many decades, some sites still do not show any vegetation (**ple-bar-59, koy-bar-54)**. Moreover, only 5 species are significantly positively correlated to age of sites. These are ubiquists and forest species. 3 of these 5 species show no significant correlation to structure. A correlation to age may indicate slow dispersal rates for these species. Hygrophilous species are significantly positively correlated to age of sites. But this is only true if the reference sites in Altsorgefeld are included in the calculation. If they are not, than there is no significance left.

Already SHAW (2003) stated that there is a general trend for species richness, diversity and density to increase with increasing age of sites. Species richness and diversity increase steadily along the chronosequence (SHAW 2003). But we also find along the chronosequence the changes in communities from meadow species to ubiquists to forest species. However, other studies on successional changes of the soil fauna demonstrated a decrease of diversity with time (DECAENS ET AL. 1998, NOWAK 2001). But already SCHREIBER (1997) concludes that every process of succession is unique in space and time.

For pH there are no significant correlations. There are negative tendencies to age and structure. This parameter is strongly influenced by melioration praxis. Sites without melioration result in low pH (< 3; MOORE & LUXTON 1988, DUNGER 1991). The tendency to decrease is caused by leaching after melioration (Figure 15, Figure 24). LIIRI et al. (2002) conclude that microarthropods at the community level are rather resistant to substantial changes in soil pH even though changes at the species level can take place. And indeed, pH 5 has been noted as landmark between 2 distinct types of Collembola communities (PONGE et al. 2003). 4 species are significantly positively correlated to pH and 10 species are significantly negatively correlated. The latter are forest species as the sites with lowest pH in this study are the three forest sites on undisturbed land. Sites without melioration and therefore low pH show only sparse vegetation with few *Calamagrostis*-plants thus resulting in low Collembola densities (DUNGER 1991). DUNGER (1989) demonstrated that under acidic mine site conditions the collembolan community changes faster and more differentiated than that of the vegetation. This could not be verified in this work. On non-acidic sites, earthworms influence collembolan succession strongly (DUNGER et al. 2004). In this study however, earthworms were never found during the researches. They are hardly abundant in the PML of Lower Lusatia.

5.3 Succession of ecological groups

Succession of ecological groups differs slightly if we look at the different levels of species or of specimens. Correlations are generally the same, but there are differences within the succession of ecological groups.

Looking at the level of dominance of species, forest species are significantly positively correlated to structure/age of sites, organic matter content, water content, water capacity, conductivity and ammonium. The reference sites of Altsorgefeld with its undisturbed woodland were treated as oldest sites in the chronosequences. Forest species were found there in great diversity, so there is a significant positive correlation to age. It is similar with structure as forest sites would be the climax in the structural chronosequence. Forest soils are rich in humus and microbial activity. Humus complexes influence water content and water capacity positively. Forest species are significantly negatively correlated to meadow species and pH as the sites of Altsorgefeld were the most acidic sites in this study, but old deciduous forests generally are (PONGE et al. 2003). Reafforestation generally leads to an increase of eurotopic species populations and strong reduction in stenotopic forest species (KOVÁC et al. 2004). This is very much true for the reclamation sites in this work, but not for the young afforestations in a larger woodland like Altsorgefeld.

Dominance of meadow species is negatively correlated to most soil parameters: stand age/structure, organic matter content, conductivity, water content, water capacity, ammonium and nitrate. There is a negative tendency to age. Open habitats like dunes, xeric grasslands and even *Calamagrostis*-dominated grassland differ totally from woodland in all said parameters. So the fact that these species are negatively correlated to structure is trivial. However, if we just look at the afforestation chronosequence, then we remember the trough or inverted Ω-shape for the number of meadow species. First, the canopy has enough gaps to let meadow species dwell at low abundances. Only after canopy closure the niches for meadows species vanish and only few can still be found. But there is an increase again at the oldest forest site. The oldest stand shows a strongly heterogeneous canopy structure. Gap fraction increases with age as was observed in other researches (WELLS & TROFYMOW 1997, 1998, TROFYMOW 2003).

Dominance of hygrophilous species is significantly positively correlated to the same parameters as are forest species but age. In addition, they are also significantly positively correlated to conductivity and nitrate. More developed vegetation structure results in better moisture conditions as was already said above. The significance in correlation to conductivity may be due to the littoral site where most hygrophilous species were found and which has high conductivity values. However, if the reference sites are excluded from statistics, then there is no correlation left. There might be some site specific effects or microsites to explain the irregular appearance of the rare hygrophilous species. HAGVAR (1982) suggests that the function of rare species may be to take over in special microhabitats or take over in the ordinary soil community during long-term changes. Very often, only one specimen in one soil core or even site is found. Either the extraction efficiency is low for several species, or a higher number of species than we know may reproduce parthenogenetically. The rare species may also be much aggregated, surviving only in certain microsites (HAGVAR 1982). Hydrophilic species were present in openings, which made the species composition somewhat puzzling in his work (PONGE 1993). Results of SHAW

(2003) indicate that hygrophilous species may perform a rapid temporary colonisation of sites after some heavy rain. So hygrophilous species may appear at regularly dry sites only temporarily and are therefore only irregularly represented in the samples. Besides, at moss-covered, otherwise dry sites hygrophilous and forest species were found in astonishing dominances.

Dominance of eurotopic species is not significantly correlated to the soil parameters. However, there is an almost significant negative tendency to age of sites. They are found at younger sites but not the youngest ones otherwise the tendency would be clearly significant. Within the chronosequence of all 30 sites tested for significances, the youngest sites are dunes and xeric grasslands whereas the oldest sites are the older woodland sites. In the forest chronosequence we find eurotopic species as dominant group when after canopy closure meadow species decrease but the habitat is not optimal for forest species to take over yet. Eurotopic species may dominate meadows, shrub land and forest (RUSEK 1989, SLAWSKI & SLAWSKA 2000). Lowest percentage of eurotopic species was found in the meadows where species typical of open land had a considerable share in the community (SLAWSKI & SLAWSKA 2000). As dominance of eurotopic species is much lower if they have to compete with another ecological group under its optimal conditions, eurotopic species might become dominant only, if there competitors are eliminated. A high tolerance for various soils is not necessarily coupled with a general high abundance (HAGVAR 1982). Here competition might have a key function. Rare species take over when they find favourable conditions in a later stage of succession (SLAWSKA 1997). PONGE et al. (2003) quote CASSAGNAU (1990) to explain their results of decrease in biodiversity in afforested former open habitats. The rarefaction of species typical of past land use is more rapid than immigration of species typical of the new environment. These results strengthen the hypothesis that eurotopic species in the woodland chronosequence become dominant when species of open habitats are already withdrawing but forest species are only beginning their immigration. In other words, eurotopic species might suffer in typical habitats from competition of better adapted species.

After studying 50 years of primary succession in the PML, DUNGER et al. (2004) conclude that collembolan communities on mine sites do not develop gradually towards a woodland community. Rather there are phases of regression (bottleneck situations). Such stages of regression were already shown for plant communities in the PML by FELINKS (2000). The results of this work support DUNGER et al. (2004) in so far as even after more than 50 years the development of collembolan communities is not towards a forest community but towards eurotopic communities.

Looking at the species level in the afforestation chronosequence we see (Table 24) that meadow species are the dominating ecological group (< 40 %) for about 23 years. After that, forest species are clearly dominating. But at the level of specimens the results are completely different. Specimens of open habitats dominate the community for 24 to 34 years (keep in mind that **koy-oak-34** was invaded by meadow specimens after adjacent clear cutting) and is then followed not by a forest community but a community of eurotopic specimens. Even after 43 years that is at the oldest reclamation site, no forest community was found at the level of specimens. But even the youngest reference site **alt-oak-29** is already dominated by forest specimens on a high level (64.6 %).

At the sites with free succession we find a much more complicated picture. On species level there is a clear dominance of most sites by species of open habitats. Exception is one bare site (**ple-bar-59**) where only few species were found and neighbouring effects have strong influence. The two oldest reclamation sites which

resemble more a clearing (**koy-den-54**) or a shrub land (**ple-den-59**) are no longer dominated by meadow species. The first site has no eudomiant ecological group whereas only at the shrub land-site forest species become eudominant. But if we look at the level of specimens again, there is no site with a dominance of forest species. The questionable bare site is now dominated by 90.9 percent specimens of open habitats. At sites with dense vegetation, we have sometimes 2 eudominant groups: specimens of open habitats and ubiquists. At least 3 of the 4 sites with 2 eudominant ecological groups differ in some soil parameters: **sch-den-8** is the littoral site, **sch-den-23** is the ash-meliorated agricultural site and **koy-den-54** resembles a clearing within larger woodland.

Specialised communities are characterised by the eudominance of a certain ecological group (KUZNETSOVA 2003). We find this supported in the afforestation chronosequence. Only if there are enough niches for forest species to reach high abundances a specialized forest community develops. In the older sites of the successional chronosequence we do not always find such a clear separation. But this does not mean that there are no specialized communities. There are specialized communities, but on a smaller scale in the PML. Best example is the littoral site **sch-den-8**. Again the level of specimens is used as the results are far more reliable. The subsamples A, C and E were always taken 0 to 1 meter away from the immediate water site following the rising groundwater table. Looking at these three subsamples closer, we find a community where no ecological group is eudominant. Both eurotopic and meadow species have a share of 37.2 % of the community. But if we go just 3 meters away from the lake site to the subsamples B, D and F, we find strong eudominance of eurotopic species (due to the strong increase of *Parisotoma notabilis* in this case). The difference in community structure within **sch-den-8** becomes obvious (figure 69). At this rather wet sampling site, no typical community of (dry) open habitats can be found. Specimens of eurotopic species take over when they find more favourable conditions 3 meters from the lake shore where it is probably still to wet for typical species of open habitats to appear in high abundances. Already MIGLIORINI et al. (2003) observed that soil communities follow soil moisture.

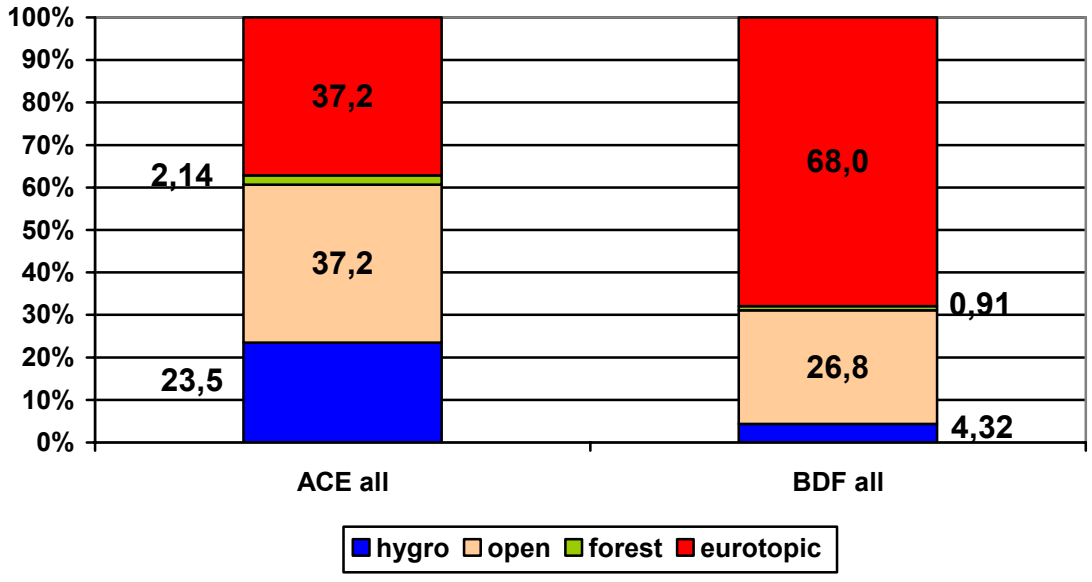


Figure 69: Two different communities at sch-den-8 depending on the distance to the lake shore.

At other sites where no specialized communities according to KUZNETSOVA (1997) were found there are no clear gradients like **at sch-den-8**. At these sites, special soil conditions (like ash at **sch-den-23**), the change from open habitat to woodland (**koy-den-54**) or other, yet unknown reasons (**cot-den-13**) prevent a single specialized community from dominating the sites.

5.4 Succession of species

In non-optimal habitats, collembolan communities have broad ranges of variation of species and ecological structures (CHERNOVA & KUZNETSOVA 2000). Important characteristics as total abundance and number of species may vary strongly not only in fluctuating communities but in stable ones also. Narrower ranges of variation may be more typical for communities in regions with a milder climate than the continental (CHERNOVA & KUZNETSOVA 2000). Highest diversity is characteristic of communities existing under conditions of environmental disturbances of medium strength (KUZNETSOVA 2003). As we find continentally influenced climate in Lower Lusatia and deal with a rather rough environment in the PML, we should find strongly varying abundances and number of species here, making interpretation of results not easier.

Succession of Collembola species is probably strongly influenced by air transport (DUNGER 1991). Coincidentally immigrating species are more dependent on soil properties and micro-climate than biotic interactions and r-strategists are favoured (ZERLING 1990). For a certain period of time (weeks, months), the soil in the dumping areas is already exposed to the air before melioration techniques are used and before researches can begin. Therefore, there are probably already some Collembola specimens contained in the soil and the soil cannot be considered as uninhabited (DUNGER 1991). This is definitely true for most sites in this work. Some sites where meliorated long after dumping because they became afforested (**sch-den-5**) or where dumped long ago, but moved again for reasons of safety (landslides) like **sch-bar-4**. However, the question remains, if the already established Collembola communities could have survived such changes or if we find a true primary succession here.

Aerial colonization by soil mesofauna takes place relatively slowly. Collembola can establish on freshly heaped mine sites within 15 months if favourable soil conditions like in Berzdorf allow for a rapid colonization (WANNER & DUNGER 2002). The question, whether surrounding “source habitats” or stochastic events influence succession, has not been clarified (WANNER & DUNGER 2002). In small “islands” of vegetation of different successional development, the effect of immigration and competitive exclusion by surrounding populations may be the primary determinants of animal community structure (PARR 1979). Diversity within a patch depends on the structure of the surrounding landscape (DAUBER et al. 2003). The findings of forest species in dunes or xeric grassland in this work indicate the significance of “source habitats” as these sites where close to pine afforestations. Moreover, the invasion of meadow species in **koy-oak-34** after adjacent clear cutting also underlines this fact. Aerial colonization from “source habitats” should therefore be studied with greater interest in the future.

Not only time since the start of the succession but also distance and direction to undisturbed areas, dispersion rates of colonisers and environmental conditions such as microclimate and vegetation structure determine the composition of successional

communities (PETERSEN 1995). It seems obvious that external factors such as spatio-temporal dynamics, boundary characteristics or neighbourhood effects also contribute to variations in species richness and community composition at the patch level (DAUBER et al. 2003). DUNGER et al. (2002) suppose that the distance to the next suitable habitats influences the immigration rate of species such as *Parisotoma notabilis*.

Armed with these pieces of information, succession of several Collembola species will be discussed and compared with other studies.

Arrhopalites caecus was found at 4 reference sites as (sub)recedent species and just once from a reclamation site (**sch-den-16**) as subrecedent species. It is rarely reported from mine sites (DUNGER et al. 2004) but described as being muscicolous (MIGLIORINI et al. 2003) and as later in succession (ZERLING 1990). As it is also said to be hygrophilous (PICHARD et al. 1989) and showed a tendency to be found at sites with higher water capacity, the generally dry PML may provide only some suitable sites like moist depressions.

Brachystomella parvula is known to be a 1st stage species (DUNGER 1975, PARR 1978), found at young afforestations (DUNGER 1989) and to colonize rapidly after fire (SHAW 1997). In this work, it was not found in the afforestation chronosequence but irregularly in the successional chronosequence. Its highest dominance was at **koy-bar-54** where it was even eudominant. It was missing at the older sites with dense vegetation. So even without statistical evidence, the mentioned observations from other studies can be underlined.

Ceratophysella succinea was regularly observed by DUNGER (1968, 1979, 1991) and DUNGER et al. (2004) as species of the 1st stage of succession. But in the PML of Lower Lusatia it is a rare species, found twice as subrecedent species (**sch-oak-23, ple-oak-43**) and once as eudominant (**cot-den-13**) on reclamation sites. It showed an almost significant tendency to be found at sites with higher pH and such sites are generally more seldom in Lower Lusatia than in DUNGER'S study area Upper Lusatia.

Cryptopygus thermophilus was found at the youngest sites with sparse vegetation as eudominant and dominant species. At sites with dense vegetation, it was found less steadily and with much lower dominance. Though no statistical evidence could be found for this observation, SHAW (2003) also found it as an early successional species on ash-sites.

Entomobrya corticalis was never found at reclamation sites. Interestingly, even at Altsorgefeld it was only found at the red oak afforestation **alt-oak-44** as dominant species (33.3 %), but missing in the younger site and only recedent at the oldest one. In other studies, it was found under bark of dead trees (FJELLBERG 1980) and to be tree climbing (DUNGER 1997). But especially at **alt-oak-44** no dead trees were found. Maybe it benefits from the exotic trees and the lack of better adapted species.

Entomobrya lanuginosa was observed by DUNGER (1975, 1989, 1991) and NOSEK (1976) as a species of initial stages of succession. This cannot be confirmed in this work. It was only found twice at older sites with dense vegetation (**sch-den-23:** 0.6 % and **ple-den-59**: 15.8 %) and older afforested sites. It would therefore be in a second or even third stage of succession.

In the afforestation chronosequence, *Entomobrya multifasciata* vanished after canopy closure, but was found again at the reference sites of Altsorgefeld, but here only dominant in **alt-oak-29** with its dense *Vaccinium myrtillus* cover. TAMM (1986) found it in an early stage of succession after fire. In the successional

chronosequence, *E. multifasciata* was found at the older sites with sparse vegetation (but not the reference site!) and most sites with dense vegetation where it was dominant to eudominant. But dominance of specimens decreased to the end of the chronosequence. It seems typical for an intermediate stage of succession.

Entomobrya muscorum was significantly correlated to structure and found at the intermediate afforestion sites at Koyne and Plessa. Unfortunately, literature does not provide us with data about its role in succession.

Entomobrya nivalis was also significantly correlated to structure. It was found only in the afforestation chronosequence and there first after 20 years irregularly as subrecedent species. TAMM (1986) noticed a rapid colonization after fire, whereas PARR (1979) called it a late species. The results here seem to confirm PARR'S (1979) statement.

Folsomia candida was first found as a subrecedent species in the afforestation chronosequence after 34 years. In both older red oak stands (**ple-oak-43, alt-oak-44**) it is a subdominant species. Interestingly, it was only found at red oak stands! *Folsomia candida* was also found at older sites with dense vegetation as recedent and subdominant species with increasing dominances. It was first found at **cot-den-13** as subrecedent species. It had a tendency to be found at older sites with better developed vegetation. ZERLING (1990) found it in a later stage of succession and it is not common in strongly disturbed areas (DUNGER 2001) but nevertheless seems to be a regular inhabitant of mine-dump soils (DUNGER et al. 2002).

Folsomia fimetaria showed an almost significant tendency to be found at sites with better developed vegetation and higher water content. For this ruderal (FELLBERG 1980, STERZYNSKA & KUZNETSOVA 1997, DUNGER 2001) and ubiquist (KOVÁC et al. 2001) species, hardly any comparable data for its role in succession are available. But ZERLING (1990) also found it as a later species in succession.

Folsomia manolachei became subdominant after 46 years of afforestation in Berzdorf (DUNGER ET AL. 2001). *Folsomia manolachei* was found only once in this work at a rather young site with sparse vegetation (**sch-spa-16**) and cannot support the observations made by DUNGER ET AL. (2001). But other authors also see it as species of (dryer) forests (PONGE 1993, CASSAGNE et al. 2004).

Folsomia penicula was first found after 23 years as subrecedent species, but later (**dom-pin-37**) as recedent and finally dominant species at the reference sites. It is generally described as mesophilic forest species (RUSEK 1995, DUNGER 2001) which prefers acidic soils. Both pieces of information could be proved in this work and it seems to be a species of the latest stages of succession.

Folsomia quadrioculata is significantly correlated to structure in this work. PARSON & PARKINSON (1986) also observed that it was positively correlated with vegetation cover. It was not found in the PML by DUNGER et al. (2004), but at more advanced stages of succession by RUSEK (2004). KOVÁC et al. (2004) found a significant positive correlation to organic matter content, soil moisture and phosphate. The significant correlation to organic matter content can be confirmed by this work's data. It was only found in the afforestation chronosequence and can be definitely considered as later species in succession. It was just once found with one single specimen on reclamation land.

Friesea mirabilis was found twice quite early as subrecedent species (**ple-pin-20, sch-oak-23**), but steadily and with higher dominances only at the oldest reclamation sites and Altsorgefeld. Highest dominance was reached at the ash-meliorated site

dom-pin-37. At red oak stands, its dominance was never more then recedent. *Friesea mirabilis* was only found at the oldest reclamation sites of the successional chronosequence and here as recedent species. At two reference sites it was found as subdominant species. It was found in a later stage of succession after fire by TAMM (1986) and in woodland or most advanced stages of succession (SLAWSKA 1997, SHAW 2003, RUSEK 2004). The missing of *Friesea mirabilis* on younger sites was probably connected with the missing aquatic soil microfauna (Nematoda, Tardigrada, Rotatoria) in unfavourable substrates of the less advanced succession stages (RUSEK 2004). It seems to be a rather late species in succession.

A *Hypogastrura*-community was discussed by DUNGER (1991) as 2nd stage community. *H. manubrialis* was also observed by PARSON & PARKINSON (1986) and SHAW (2003) as early successional species. RUSEK (2004) found *Hypogastrura assimilis* as species typical of early succession. But the only *Hypogastrura* species found in this work was *H. manubrialis.* It was found only once (**sch-den-23**) as subdominant species, so it does not seem to play a prominent role in succession in Lower Lusatia.

Isotoma anglicana was found early on sites with sparse vegetation. Its dominance declines towards the end of the chronosequence. *Isotoma anglicana* is algivorous and missing in his work at sites where light conditions do not favour the development of algae (RUSEK 1992). This was also observed in this work, where the species was missing after canopy closure in the older reclamation sites of the forest chronosequence. It was observed by ZERLING (1990) as species of the 1st stage of succession. Results hint at a second stage position.

Isotoma viridis is found only at sites with dense vegetation, mainly at the oldest sites although it benefits from wind drifting (DUNGER et al. 2002) and should therefore be expected at younger sites. It was observed as a species of the 1st stage of succession by DUNGER (1991) and PARSON & PARKINSON (1986) also found it at newly reclaimed coal shales, but TAMM (1986) describes it as a later species after fire. Own results also see it as a later species in Lower Lusatia.

Isotomiella minor was found at most afforestation sites but the youngest ones. Here, it was first recorded from **ple-pin-20**. But it is was only once (at the moss-rich site **sch-spa-19**: subdominant) more then a (sub)recedent species on reclamation sites. Only at Altsorgefeld it is a dominant and even eudominant species. The occurrence at **ple-pin-20** for the first time in the chronosequence might be due to the fact that at this site, age of soil is considerably older than stand age (s. chapter 3.3). In other studies, it was found in later (ZERLING 1990) and at the most advanced stages of succession (RUSEK 2004). KOVÁC et al. (2004) found a significant correlation to structure, which was also found in this work. Besides, a significant negative correlation to pH was found which might explain why LIIRI et al. (2002) found that *Isotomiella minor* was less abundant in ash-treated soils. This was not observed here: *I. minor* was found at both ash-meliorated sites although just as [sub]recedent species, but it is generally only a subrecedent to subdominant species on reclamation sites anyway in Lower Lusatia.

Isotomodes productus is reported to be a 2nd stage species (DUNGER 1989, ZERLING 1990). It is a very rare species in this work: Twice subrecedent on reclamation land with dense vegetation (**sch-den-8, sch-den-**23) and subdominant once at **sch-den-ref2**. It is significantly correlated to pH and for lack of sites with high pH at a later stage of succession it is a rare species in the PML of Lower Lusatia. The observation of DUNGER et al. (2001) that it became subdominant after 46 years of afforestation

can therefore not be supported by this study although SHAW (2003) also found it at the woodland stage of succession.

Already in 1991 DUNGER said *Lepidocyrtus cyaneus* to be a 3rd stage species (first shrubs and bushes). This was confirmed by SHAW (2003). Also TAMM (1986) noticed its long absence after fire. Yet in this work, it was found at the oldest sites with sparse vegetation, most sites with dense vegetation and missing at most forest sites. These observations are more according to ZERLING (1990) who put it in a 2nd stage of succession in open landscapes. It was significantly correlated to nitrate in this study.

RUSEK (2004) observed that more advanced communities contained *Lepidocyrtus* lanuginosus. DUNGER (1991) and IRMLER (1996) however found *Lepidocyrtus lanuginosus* as a 1st stage pioneer and not as one of the more advanced stages. Results of this work support RUSEK (2004), as *L. lanuginosus* is significantly positively correlated to structure and was found only at sites with dense vegetation and some afforested sites.

Lepidocyrtus lignorum was almost exclusively found at sites with dense vegetation and 20 to 43 years old afforestations on reclaimed land as subdominant to dominant species. It showed a tendency to be found at older sites. Already PARR (1979) called it a late species.

Lepidocyrtus paradoxus was only found once and not at a reclamation site. It was found at **sch-den-ref1** as eudominant species. It had been had been viewed as a 1st stage species (DUNGER 1991) and registered in earliest stages in afforestations (DUNGER 1997). DUNGER et al. (2001) call it a dominant and characteristic species for early succession.

Megalothorax minimus was never found outside the oldest reference site in Altsorgefeld in this work so never on reclamation land. In other studies, it was found at the most advanced (forest) stages of succession (SLAWSKA 1997, RUSEK 2004, KOVÁC et al. 2004). Already PARR (1979) called it a late species. It became a subdominant species after 46 years of afforestation on mine soil (DUNGER et al. 2001).

Mesaphorura atlantica is dominant in the younger pine afforestations with their missing herb layers, but missing at the youngest **site sch-den-5** with its dense vegetation cover. In the successional chronosequence, *Mesaphorura atlantica* has again a negative correlation to structure. It was found at all sites **without** dense vegetation but one (**sch-spa-16**), but with changing dominances from > 90 % at **ple-bar-59** to about 5 % at **sch-spa-19**. It was a dominant species at a reclaimed English coal area (LUXTON & MOORE 1988) and observed at the Rhineland mining area (SCHULZ, pers. Comment). It was identified as pioneer species by RUSEK (2004). It exact position will be discussed later using the cluster trees.

Mesaphorura critica was found at all types of structure but afforested sites with closed canopy. Its highest dominance was reached at the moss-rich reference site **sch-spa-ref** (77.6 %). Its distribution did not allow for a statistical correlation. Yet it seems to prefer the earliest stages of succession and becomes less abundant and decreasing in dominance at sites with dense vegetation ar woodland stages. ZERLING (1990) observed that it was later in succession which cannot be confirmed by my results.

Mesaphorura italica is an extremely rare species in the PML of Lower Lusatia. It was just found once at **sch-den-ref1** as subrecedent species. DUNGER (1997) observed that it preferred red oak afforestation over pine in Domsdorf. ZERLING (1990) found it

in a later stage of succession, but as it seems to be a very rare species in Lower Lusatia, no new knowledge can be added to the discussion.

Mesaphorura hylophila was found in a more advanced stage by RUSEK (2004). ZERLING (1990) observed that it was abundant in almost all successional stages in reclaimed land after lignite mining. In this work, it was also found at all stages of succession but the very first ones without any vegetation. However, it was just once a subdominant species at **sch-den-ref1** and (sub)recedent at all other sites. Like the former species, DUNGER (1997) observed that it preferred red oak stands over pine stands in Domsdorf. The position of this species remains unclear.

Mesaphorura krausbaueri was found twice at sites with dense vegetation, **cot-den-13** as recedent species and **sch-den-ref2** as subdominant species. It had not been found in the PML by DUNGER ET AL. (2004). It shows an almost significant tendency to be found at sites with higher pH, confirming PONGE (2000) who called it acidointolerant. It seems to be a species of a later stage in succession.

Mesaphorura macrochaeta is eudominant (50 % to > 80 %) in the afforestation chronosequence for 34 years and then becoming suddenly only dominant with gradually declining dominance values. Dominance for decades of this species was already observed by DUNGER (1991). It was viewed as 1st stage species in succession (ZERLING 1990, DUNGER 1994, KRAWCZYNSKI & BRÖRING 2004), but data from this work put the species in a later stage of succession. In the successional chronosequence, its dominances vary strongly; highest dominances were found at younger sites, but the correlation is not significant. The tendencies to be found at sites with higher organic matter content and water content propose an intermediate position in succession. Its position will be discussed using the results of the cluster trees.

Mesaphorura tenuisensillata was rarely reported from mine sites (DUNGER et al. 2004). It remained an eudominant species in Berzdorf after 46 years of afforestation (DUNGER et al. 2001). In this work, it was just found once at **sch-den-5** as subrecedent species at quite a different habitat.

Micraphorura absoloni was just once found at the successional sites (the moos rich site **sch-spa-19**), here even as dominant species (14.3 %). At Altsorgefeld, its dominance increases constantly with age and is eudominant at the oldest site. It is significantly negatively correlated to pH. This is according to literature, where it is described as acidophilious (PONGE 2004) forest species (SLAWSKI & SLAWSKA 2000, FJELLBERG 1998).

Micranurida pygmea is said to be a 2nd stage species (DUNGER 1989) and found at the earliest forest stages (DUNGER 1997). It decreased considerably after 46 years of afforestation (DUNGER et al. 2001). LIIRI ET AL. (2002) found that *Micranurida pygmea* was less abundant in ash-treated soils. *M. pygmea* was not found at the two ash-meliorated sites in this study, but as it occurred with an irregular pattern anyway, it would be careless to associate it with ash-melioration. Moreover, data do not provide us with enough information in this work to make a reliable statement about its position in succession.

Neanura muscorum and *Orchesella flavescens* were found at the oldest reclamation sites and Altsorgefeld. TAMM (1986) observed a long absence of *N. muscorum* after fire. DUNGER et al. (2001) also found *O. flavescens* at woodland stages of succession and 40 years old dumps with deciduous forest (DUNGER 1989). But *O. flavescens* shows a specific decline in dominance: At **dom-pin-37** it appears for the first time

and is already eudominant (41.7 %), but declines on the following sites. At least still subdominant at the oldest reclamation site, it becomes barely recedent at all Altsorgefeld sites. Both species were only twice found at the successional sites with dense vegetation, *N. muscorum* as subdominant and recedent and *O. flavescens* both times as subrecedent. *Orchesella flavescens* was found only at the two oldest afforested sites and Altsorgefeld.

Paratullbergia macdougalli was only found at the three young pine afforestations, but missing at all oak sites and the older pine site **dom-pin-37**. In contradiction, DUNGER (1997) found *P. macdougalli* at Domsdorf in red oak stands and not in pine stands. It is generally found in leaf litter (FJELLBERG 1980), prefers probably moist and wet sites (DUNGER 1994) and is not abundant (DUNGER 1997). Its said preference for moist or even wet sites might be the reason for this species missing at most sites in the generally dry PML.

Parisotoma notabilis was found at some sites without or sparse vegetation. But it was always found with generally higher dominances at sites with dense vegetation. KUZNETSOVA (in press) also found it as dominant species in a natural dry meadow. DUNGER et al. (2002) observed stable populations of *Parisotoma notabilis* after 4 months of succession. The species seems to have a well developed dispersal ability and was also found at the youngest sites in this work, but only with low dominances. It was observed as a 2nd stage species in succession (DUNGER 1968, ZERLING 1990, KRAWCZYNSKI & BRÖRING 2004), but most recent works including this one group it in a later stage of succession. DUNGER et al. (2004) link it with the first accumulation of litter and in this work an almost significant tendency was observed for the species to be found at sites with more developed vegetation structure (and therefore litter). Moreover, *Parisotoma notabilis* is known to appear in (earliest) woodland stages of succession (DUNGER 1997, SLAWSKA 1997, SHAW 2003) and oldest sites of pine afforestations (JUCEVICA & MELECIS 2002).

Proisotoma minima was found at two sites with dense vegetation and some of the older afforestation sites, but always as subrecedent species. This indicates a later stage in succession whereas DUNGER et al. (2002) views it as 1st stage species.

Proisotoma minuta decreased considerably after 46 years of afforestation in Berzdorf (DUNGER et al. 2001). *Proisotoma minuta* and *Isotomodes productus* were significantly often found together in this work although *P. minuta* was subdominant at those sites and *I. productus* barely subrecedent. Both species are also significantly correlated to pH. The Lower Lusatian PML lacks sites with high pH. However even without statistical proof, *P. minuta* was generally found at sites with sparse vegetation and already DUNGER (1989) and ZERLING (1990) declared it to be a 1st stage pioneer species. But *Proisotoma minuta's* role in succession in Lower Lusatia will be discussed later using the cluster trees.

Protaphorura armata is significantly positively correlated to structure in this work. DUNGER et al. (2001) found it as subdominant species after 46 years of reafforestation in Berzdorf. At undisturbed sites, it is found in various habitats (FJELLBERG 1998), coniferous forests (HAGVAR 1982), preferably under beech (CASSAGNE et al. 2004), lawns (ROCHEFORT et al. 2006) or dominant in meadows (KUZNETSOVA, in press). In this work it was found at three sites with dense vegetation, the oldest afforested reclamation site and all three sites of Altsorgefeld. It is most probable a late species in succession.

Pseudoanurophorus alticolus was found at open dry habitats with weakly developed vegetation in this work. There are significant negative correlations to most soil

parameters like structure, organic matter content and water indicating an early position in succession. It was significantly often found with *Mesaphorura atlantica*, therefore it might also be acidophilous.

Schoetella ununguiculata was mainly found at sites with sparse vegetation and in the early forest stages. RUSEK (2004) also found it in the early stages of succession but DUNGER (1989) at afforested dumps. But this work's significant negative correlation to most soil parameters like age, organic matter content and water indicate a very early position in succession.

Sminthurinus aureus was found as subdominant species at sites with dense vegetation. It was generally missing at sites without dense vegetation. In the afforestation chronosequence it has a very irregular pattern and even becomes eudominant once at **koy-oak-34** which had been disturbed by adjacent clear cutting. DUNGER et al. (2001) found it at the woodland stage of succession and this might be confirmed by the fact that it is significantly positively correlated to organic matter content.

Sphaeridia pumilis was only found at sites with dense vegetation and there generally as dominant species. In the afforestation chronosequence the pattern is very irregular and it is never more than a subdominant species. It was observed in young afforestations by DUNGER (1989) and may therefore be regarded as species of a more advanced succession.

Tomocerus flavescens was found in later stages with dense vegetation. DUNGER et al. (2001) observed that it became dominant when the grassland stage turned into woodland and so support the observations made in this work. In an earlier work, DUNGER (1989) found it at a 40 years old dump with deciduous forest. Already TAMM (1986) noted its long absence after fire. This may be due to poor dispersal abilities.

Tomocerus vulgaris was found three times at reclamation sites and never at the reference sites. Sites were with sparse vegetation (again the moss-rich site **sch-spa-19**), red oak afforestation (**koy-oak-24**) and pine afforestation (**dom-pin-37**). There are not enough data to draw conclusions towards its role in succession, but TAMM (1986) observed it in a later stage of succession after fire.

After comparing data with literature, a rough model can be offered for succession of epigaeic species in Lower Lusatia (fig. 70). Generally, "initial", "pioneer" and "woodland" groups are discernable (DUNGER et al. 2004). But maybe a more precise model can be suggested.

Statistic evidence used in this work should provide with data about succession. Species which are significantly negatively correlated to parameters like structure, age, organic matter content, conductivity, water content and capacity should be true xeric species and found at the very beginning of succession on the poorest soils. On the other hand, species significantly positively correlated to these parameters or never found on reclamation land, should indicate climax species in the sense of linear succession.

As there is not always statistical evidence for the species position (Spearman Rho, cluster trees), this model cannot be as precise as the following one for endogaeic succession. Nevertheless, up to five different stages of succession can be found, according to vegetation structure. The problem we are facing here is that other authors are quite free in describing a species' position in succession. Sometimes they give only rough information like later stage or most advanced stage (RUSEK 2004, KUZNETSOVA in press) on non-mining sites and long-time chronosequences.

Others have short-time chronosequences like TAMM (1986) who studied 5 years of succession after fire in a forest and give information, if it is an “early” or “late” species. Again others like DUNGER (1989) or ZERLING (1990) divide succession on mining-sites after long-time chronosequences in a number of stages without a comparable definition to foresaid authors. A fith stage of old forest as reference on non-mining sites is generally missing.

In this work, the 1st stage is defined as sites without vegetation. Species found here are *Pseudoanurophorus alticolus, Schoetella ununguiculata, Bourletiella pruinosa* and *Brachystomella parvula*.

At the 2nd stage, already some sparse vegetation can be found. Some sites are also covered densely by moss. Here, *Cryptopygus thermophilus, Isotoma anglicana* and *Lepidocyrtus cyaneus* are found for the first time.

The 3rd stage is defined as sites with dense vegetation, generally *Calamagrostis epigejos* dominated sites. Oldest sites have already some shrubs made of young pines or are clearings in young woodland. Several species are found here for the first time in notable dominances: *Entomobrya lanuginosa, Entomobrya multifasciata, Lepidocyrtus lignorum, Isotoma viridis, Lepidocyrtus lanuginosus, Sminthurinus aureus, Sphaeridia pumilis* and *Tomocerus flavescens.*

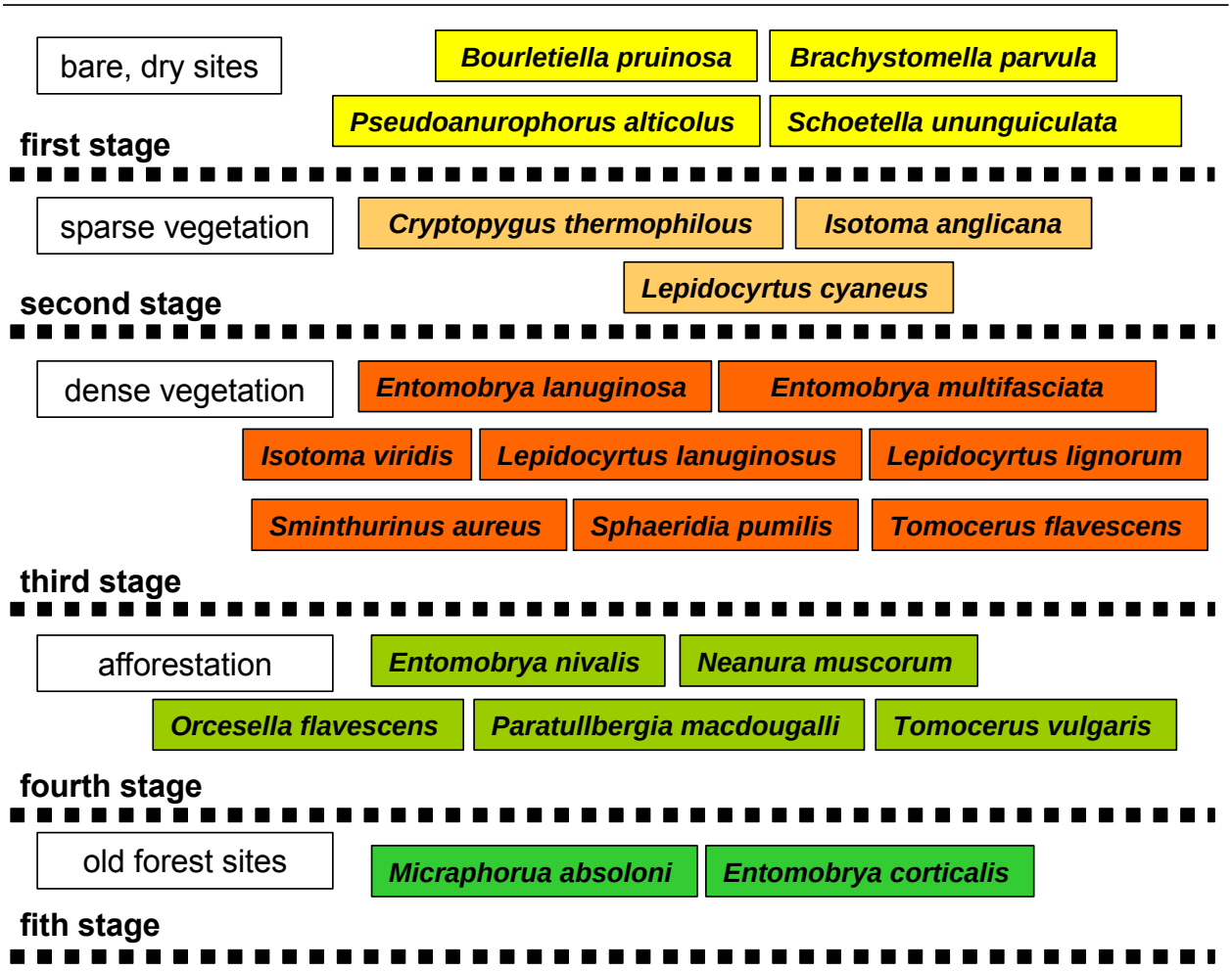


Figure 70: Model of epigaeic succession.

The fourth stage is made up by afforestations up to 43 years on reclamation sites. 5 more species are found here: *Entomobrya nivalis, Neanura muscorum, Orchesella flavescens, Paratullbergia macdougalli* and *Tomocerus vulgaris.*

The 5th stage would be the climax stage, an old oak forest. It is probably not comparable to a true primeval forest, but the type of forest typical for today's mining sites. Only 2 species were found here: *Micraphorura absoloni* and *Entomobrya corticalis* (fig. 70)**.**

5.5 Succession of endogaeic key- species

Cluster trees arranged sites according to the dominant endogaeic species. So it is probably true that the endogaeic community is much more reliable for such researches as REBEK et al. (2002) and CHAUVAT et al. (2003) already stated. The cluster trees (figures 47 and 67) separated study sites by there edaphic communities. Communities were defined by *Folsomia penicula, Isotomiella minor, Mesaphorura atlantica, Mesaphorura macrochaeta, Proisotoma minuta* and *Parisotoma notabilis.* This group of species will be further on called "key-species".

Mesaphorura atlantica was found at English coal shale reclamation sites (MOORE & LUXTON 1986) and later in the Rhineland on lignite reclamation sites (SCHULZ, pers. comment). RUSEK (2004) found it as early species in his work. By the results of this work, it seems most likely that *M. atlantica* is among the earliest colonisers of reclamation sites in Lower Lusatia. It colonizes the sites earlier than its sibling *M. macrochaeta* which was up to now regarded as pioneer species. *Proisotoma minuta* is also regarded to be a pioneer species (DUNGER 1968, 1989, ZERLING 1990, DUNGER et al.2002) and to colonize soils as the very first species. Cluster analysis for the successional sites (fig. 66) shows that there are 2 different kinds of early succession: One community is characterised by *Mesaphorura atlantica*, the other by *Proisotoma minuta*. The *M. macrochaeta* community follows in a 2nd step and may last for decades.

***Mesaphorura atlantica*-community:** The *Mesaphorura atlantica* community is most typical for sites without vegetation especially vascular plants, but sites may be covered by moss or pine litter. It may be accompanied by *M. macrochaeta* which can be co-dominant. These sites have a mean pH between 3.5 **(sch-bar-00**) and 4.3 (**ple-bar-59**; tab. 11). The sites at which MOORE & LUXTON (1988) found *M. atlantica* had a pH as low as 2.7, similar to Altsorgefeld with a pH of 2.9 (tab. 1) where *M. atlantica* is still a recedent species. Moreover, at sites which were treated with lime i.e. with an increased pH, *M. atlantica* was no longer dominant in England (MOORE & LUXTON 1988). At the afforested sites the species was only dominant at sites without either herb layer or well developed humus layer, but already *M. macrochaeta* is eudominant at such sites. Most specimens were found at sites with a pH between 3.8 and 4.8. *M. atlantica* may therefore be regarded as acidophilic species.

The *M. atlantica* community seems to lead over to the *M. macrochaeta* community on acidic sites (figure 73).

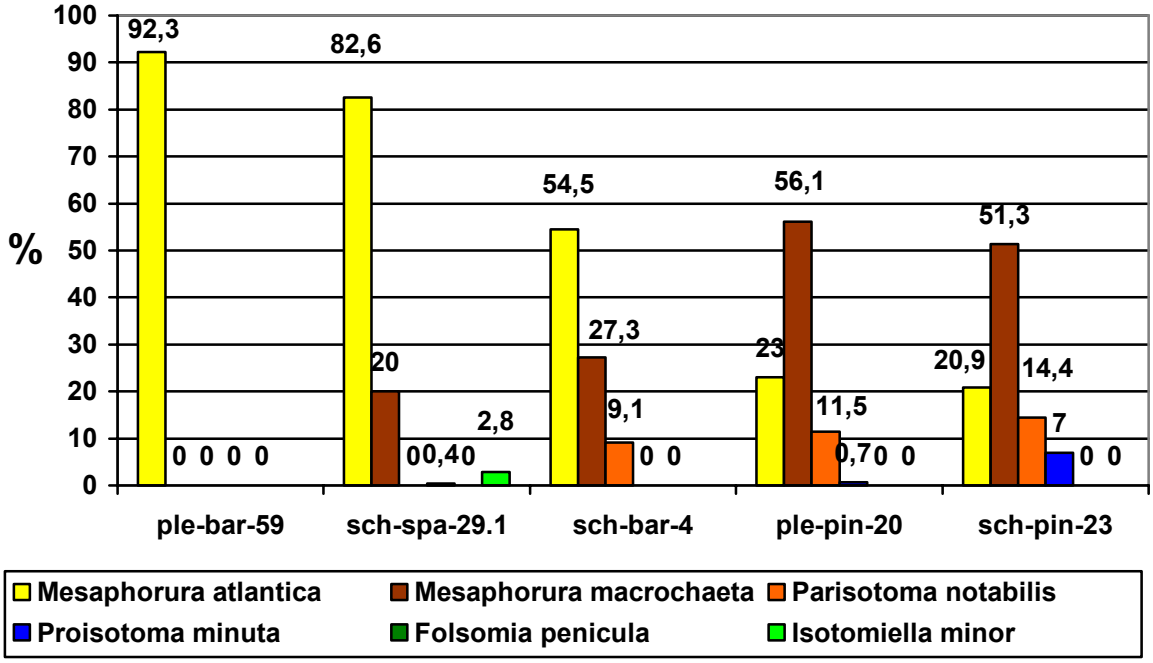


Figure 71: Dominance structure for the key-species on sites with *Mesaphorura atlantica* dominance.

Significantly often found with *Mesaphorura atlantica* was *Pseudoanurophorus alticolus* of the epigaeic community.

***Proisotoma minuta*-community:** This community is not easily found as "pure" community in this work. When looking at the total results of the study sites, it never becomes eudominant and is mainly subdominant. An example is **sch-spa-16** which is a more or less homogenous sampling site. Here, the edaphic community is almost exclusively made up by 2 species: a dominant *P. minuta* and a eudominant *Mesaphorura macrochaeta*. Eudominance of *P. minuta* is only found at certain subsamples, where soil conditions differ from the rest of the study site. At **sch-spa-29** *P. minuta* is the dominant species but is even eudominant at the frequently disturbed and sparse subsamples A + B: The site **sch-spa-29** (1/3 almost without vegetation, 2/3 with a young *Calamagrostis epigejos* stand) is characterised by 2 different communities: A clean *Proisotoma minuta* community is dominating the subsamples with very sparse vegetation with *M. atlantica* and *Parisotoma notabilis* as accompanying subdominant species. A *Mesaphorura macrochaeta – Parisotoma notabilis* community characterizes the part with dense vegetation with *P. minuta* and *M. atlantica* as recedent species (fig. 72).

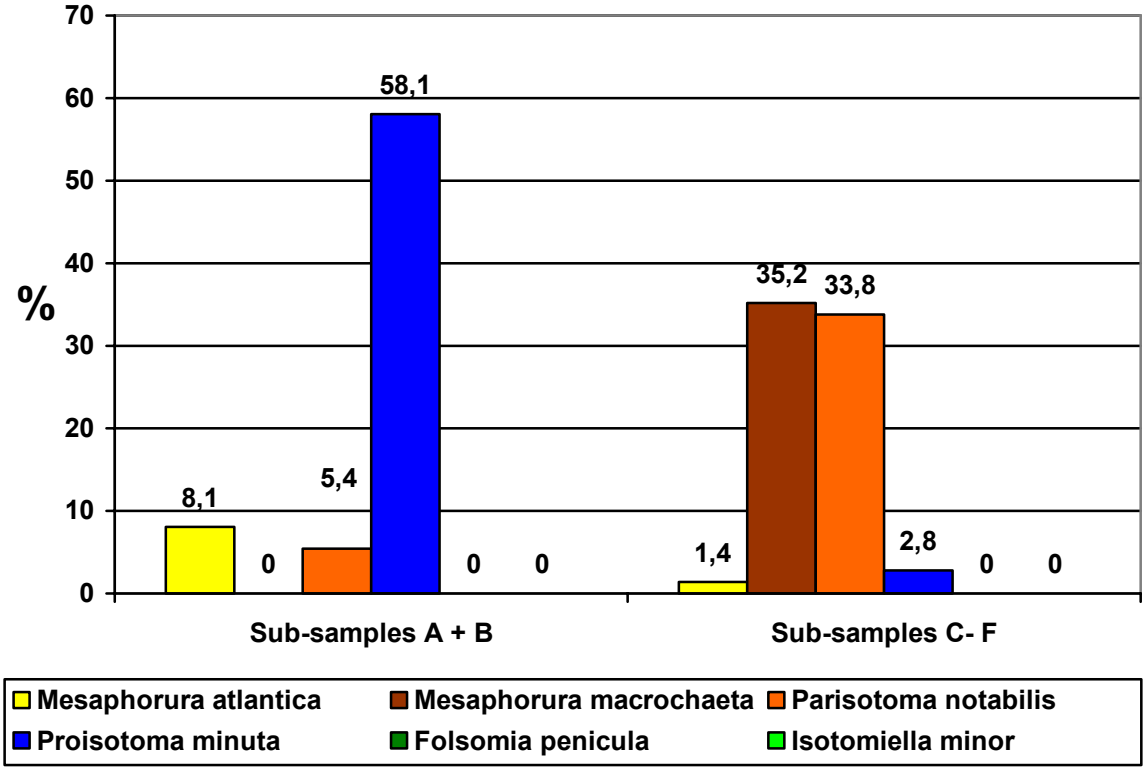


Figure 72: Two different Collembola communities at sch-spa-29**. The subsamples A and B are frequently disturbed by wild boar and covered with hardly any vegetation at all. They are characterized by *Proisotoma minuta* as eudominant species. The subsamples C to F in a *Calamagrostis epigejos* stand are characterised by a *Mesaphorura macrochaeta - Parisotoma notabilis* community.**

Another example is **sch-den-8:** At the three subsamples, which are immediately to the lakeshore, *P. minuta* is eudominant with *P. notabilis* as dominant species. But only three meters farther, *P. notabilis* is almost exclusively present in the edaphic community (fig. 73).

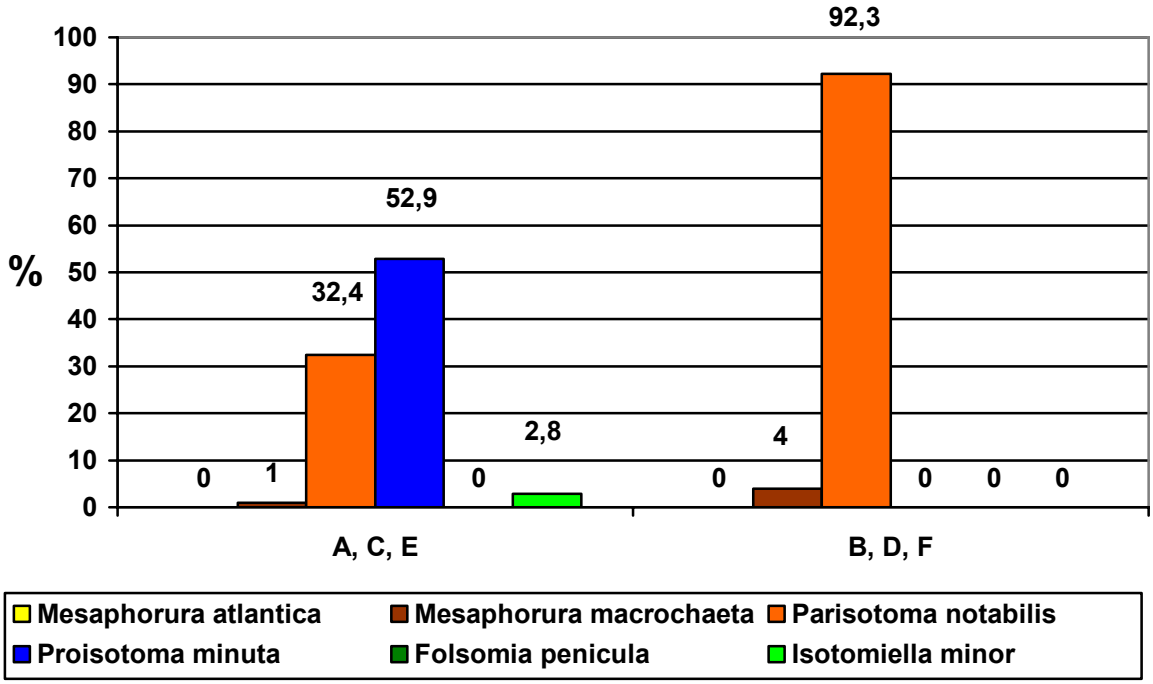


Figure 73: Two different Collembola communities at sch-den-8**. Subsamples A, C, E are *P. minuta community*, whereas the subsamples B, D, F are a *P. notabilis* community.**

So the *P. minuta* community may either be "pure" like in **sch-den-29 A+B**, or leading over to the *Mesaphorura macrochaeta* community (**sch-spa-16)** or to the *Parisotoma notabilis* community (**sch-den-8 A, C, E**; fig. 74). Sites with *P. minuta* eudominance or at least strong dominance are marked by high pH values (from 6.1 to 7.4). So if *P. minuta* really was a 1st stage species (DUNGER 1989, ZERLING 1990) it is acidointolerant whereas *M. atlantica* as another 1st stage species is acidophilous (MOORE & LUXTON 1988). Thus, pH separates both species as pioneers.

But it is also known that *P. minuta* can build up communities for decades under generally unfavourable conditions (DUNGER 1991). Such conditions may be slurry polluted soils (DUNGER 2001) like at **sch-den-8** or frequent disturbance like at **sch-spa-29.** For natural biotopes in Central Europe it is a highly uncommon species (DUNGER 2001). In Lower Lusatia, it may be a 1st stage pioneer on sites with high pH and replace *M. atlantica* there, but may also outlast for some years if soil conditions are unfavourable for generally succeeding species.

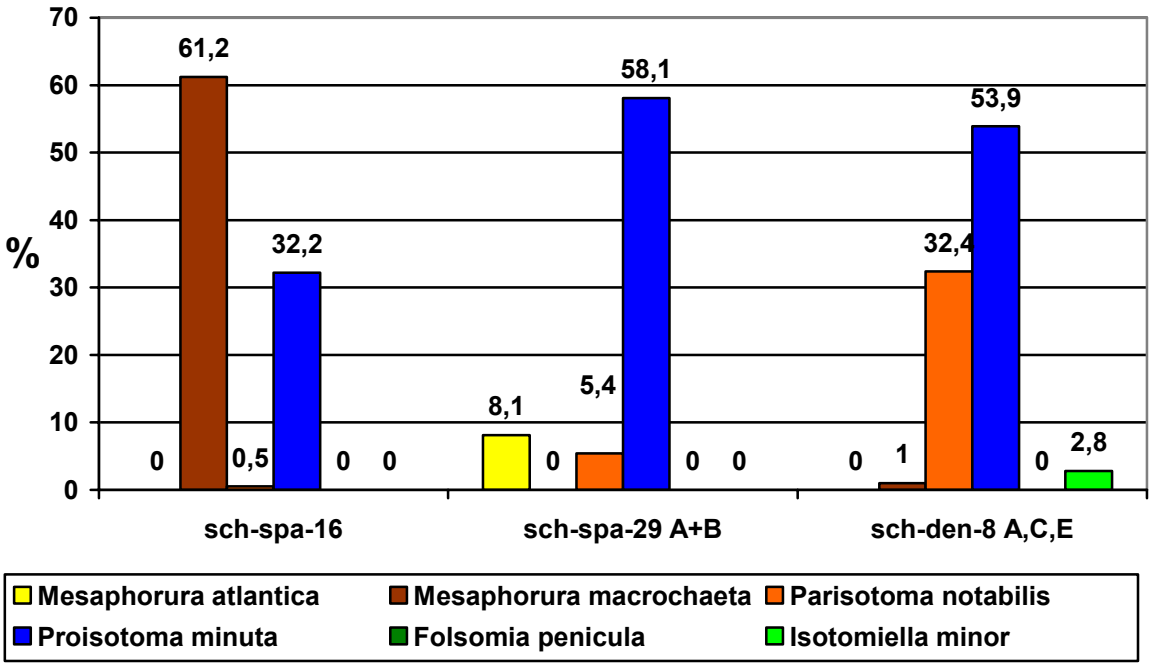


Figure 74: Dominance structure for the key-species on sites with *Proisotoma minuta* dominance.

Mesaphorura macrochaeta-community:

Mesaphorura macrochaeta was found at sites with all type of structure. As pH is a land mark for Collembola (PONGE et al. 2003) and was already proved for *M. atlantica*, maybe pH helps to explain the irregular dominance pattern of *M. macrochaeta.* At sites where *M. macrochaeta* is eudominant, pH varies from 4.0 at **koy-bar-54** to 7.3 at **cot-spa-4** which covers almost the whole range of pH in this work. So pH does not separate this community from both 1st stage pioneer communities. In addition, it is eudominant at a site bare of vegetation (**koy-bar-54**). Vegetation structure does not seem to play an important role either. So may *M. macrochaeta* itself be a pioneer species? There were no significant correlations to soil parameters found in this work, only a tendency to be found at sites with higher organic matter content and higher water content. This contradicts the idea of *M. macrochaeta* being a pioneer, as a true pioneer it would have to be negatively correlated to these parameters. And indeed, **koy-bar-54** had an unusual high organic matter content (7.24 %) which is due to a high amount of remaining lignite. But what influence does remaining lignite have on Collembola? The question will have to be answered later. At least, the *M. macrochaeta* community seems to lead continuously over to the *Parisotoma notabilis* community (figures 75 and 76).

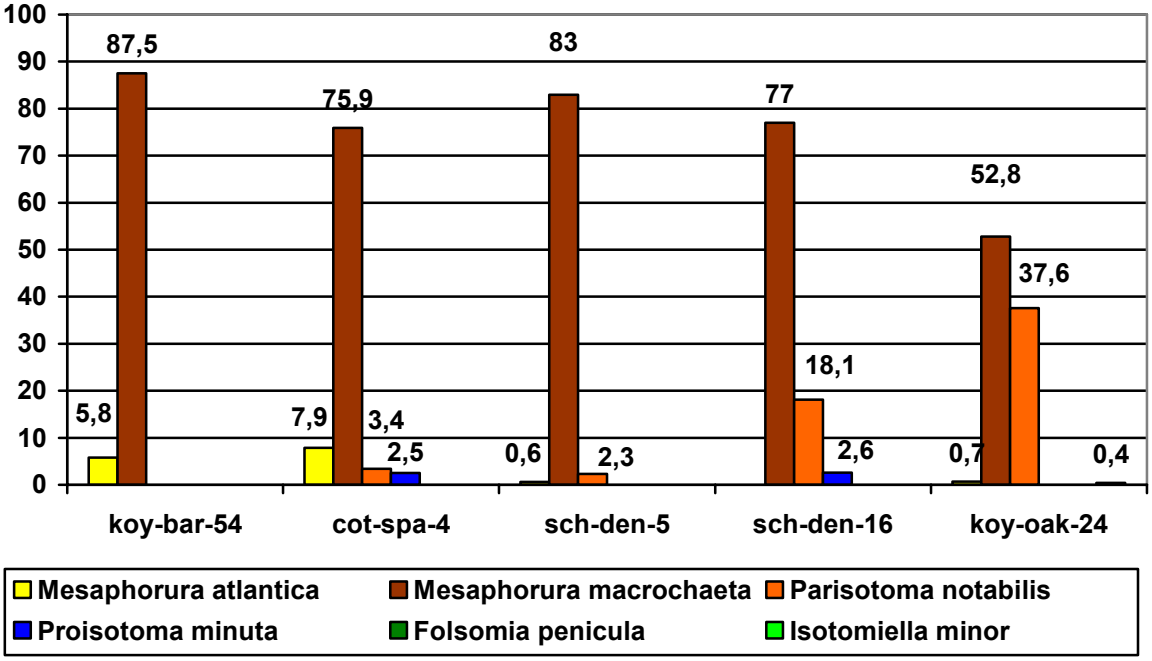


Figure 75: Sites where *M. macrochaeta* is eudominant and the other key-species in comparison.

Parisotoma notabilis-community

Parisotoma notabilis was never found as eudominant species at sites without dense vegetation or older forest sites. It only showed an almost significant tendency to be found at sites with more developed vegetation, indicating that it is neither a pioneer species nor a climax species but somewhere in between (fig. 76).

There is a significant negative correlation to *M. atlantica* indicating that both species are excluding each other. *M. macrochaeta* only shows a tendency to be found at sites with higher organic matter content, but *P. notabilis* is significantly correlated to organic matter content (cf. DUNGER et al. 2002), thus indicating a 3rd stage in succession after *M. atlantica* and *M. macrochaeta*. This contradicts PARSON & PARKINSON (1986) who found *P. notabilis* as initial colonizer on English coal heaps. Interestingly, the high dominance over *M. macrochaeta* at the afforested sites is only at the oldest reclamation sites, confirming its position after *M. macrochaeta*. But on the reference sites of Altsorgefeld, *M. macrochaeta* has a higher dominance again although both species are merely (sub)dominant and declining with stand age.

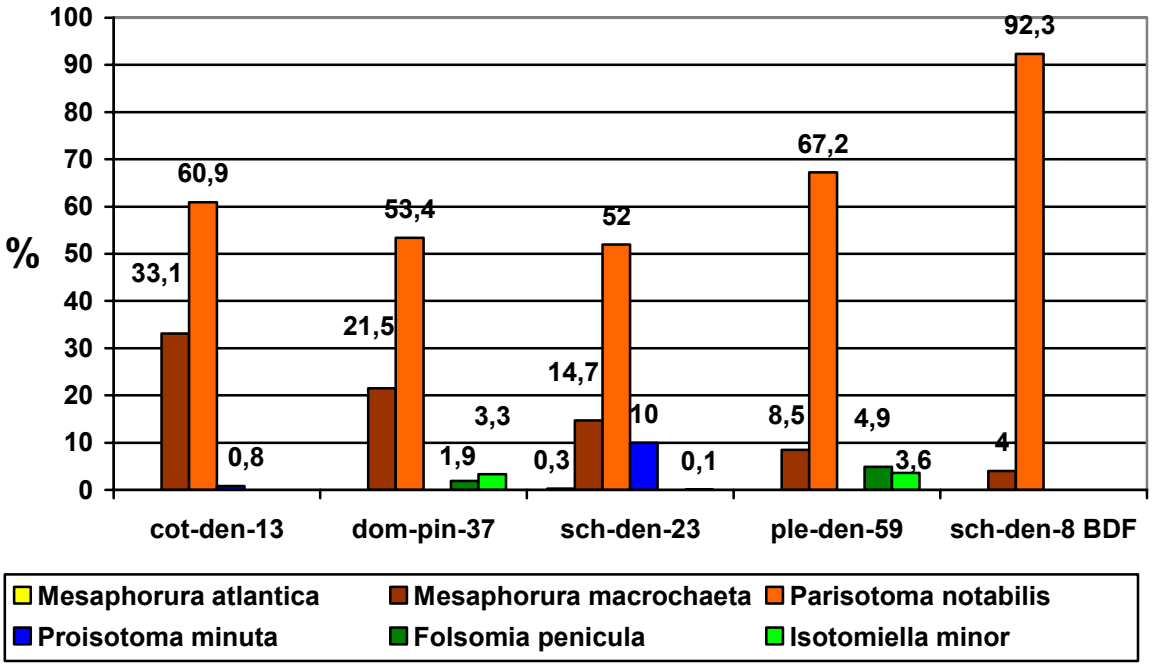


Figure 76: Sites where *Parisotoma notabilis* is eudominant and the other key-species in comparison.

Folsomia penicula – Isotomiella minor-community

At the Altsorgefeld sites, another community takes over, the *Folsomia penicula – Isotomiella minor* community. Dominance of *F. penicula* decreases with stand age and *I. minor* becomes eudominant at the oldest reference site (figure 77). It is hard too say from the data, if we really deal with just one or two communities here. Either way, the community is the most advanced in this work, with many accompanying species which were only found here (like *Megalothorax minimus, Mesaphorura yosii* or *Metaphorura affinis*). Data would suggest a transition to a *Parisotoma notabilis* community as earlier stage in succession. At the oldest successional site with eudominance of *P. notabilis*, *Folsomia penicula* and *Isotomiella minor* are already present (figure 76). But as even the oldest reclamation sites of the afforestation chronosequence differ strongly from the reference sites at Altsorgefeld, there might be a missing link between both communities. Older sites should be studied more deeply in the future to find proves for the transition between the *Parisotoma notabilis* and the *Folsomia penicula – Isotomiella minor* communities. Both (sub?)communities share most accompanying species. But each has some exclusive species and may therefore be just two very closely related and interacting communities (figure 78).

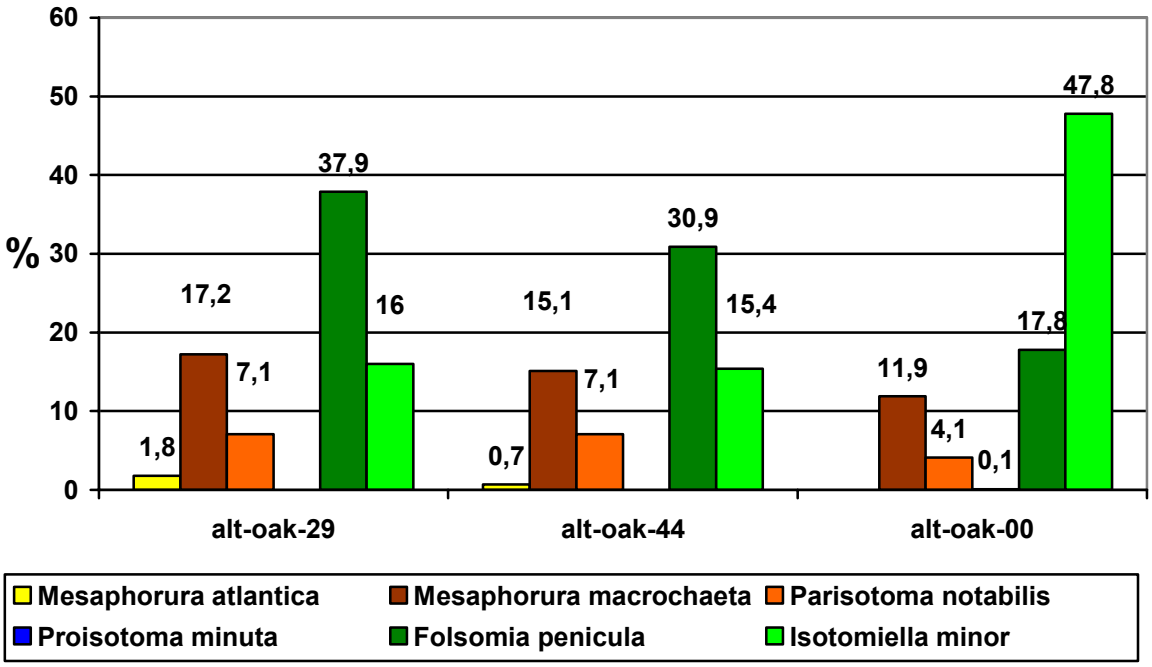


Figure 77: Sites with dominances of *Folsomia penicula* and *Isotomiella minor*, other key-species in comparison.

Five different communities could be distinguished so far:

- *Mesaphorura atlantica* dominated as true pioneer species at sites with low pH
- *Proisotoma minuta* as pioneer species at sites sites with high pH
- *Mesaphorura macrochaeta* dominated as a second stage in succession
- *Parisotoma notabilis* dominated as a third stage in succession
- *Folsomia penicula – Isotomiella minor* dominated as most advanced stage.

Both pioneer communities are poor of species. Both were found significantly often with just one other species each. The epigaeic *Pseudoanurophorus alticolus* forms the community with *Mesaphorura atlantica* on bare, dry and acidic sites. There seems to be just one pathway of succession to the *Mesaphorura macrochaeta* community on dry and mesic sites, if (mykorrhiza)fungi are present. This may be due to plant roots or due to fungi on remaining lignite.

The endogaeic *Isotomodes productus* is the single species in the *Proisotoma minuta* community. It is typical for basic sites (VAN STRAALEN & VERHOEF 1997) with already sparse vegetation. Soil may be moist to wet. On merely moist sites, the *Mesaphorura macrochaeta* community follows in a second step of succession. But on wet sites with slurry soils, the *Proisotoma minuta* community may persist for many years in then dense vegetation and may itself also cover the second step in succession. There it leads over to the *Parisotoma notabilis* community. Both communities share *Isotomodes productus* as common species (fig. 78).

As second stage follows the *Mesaphorura macrochaeta* community and again, there is just one species significantly correlated to this community: *Willemia anophthalma*. In just very few cases, when enough remaining lignite is colonized by mykorrhiza fungi, this community could be viewed as a first stage colonizer. But as it takes some years for fungi to colonize the lignite, it may be doubtful if this is a true first stage succession. The relationship between lignite colonizing fungi and *M. macrochaeta* should be a field for future research. The more typical second stage of succession is found at sites with a vast range of soil properties from dry to mesic sites, acidic to basic, sand to loamy sites. But all sites already have some vascular plants in at least sparse structure. After vegetation develops a dense structure, it leads over to the *Parisotoma notabilis* community as a third stage of succession. At afforested sites, the picture is less clear. It seems to lead over to the *P. notabilis* community after some thirty to forty years of afforestation. However, *W. anophthalma* is not part of the *P. notabilis* community, but part of the more advanced *Isotomiella minor* community. However, the reference site **sch-spa-ref** is dominated by a *Mesaphorura critica* community. It has been noted that after disturbance a primary edaphic coenoses with its climax communities is replaced by less native ones that rapidly colonise these sites due to their great dispersion capacity and high productive rates (USHER et al. 1982, MIGLIORINI et al. 2003). The *M. macrochaeta* community on reclamation sites with sparse vegetation might be an example for such a replacement.

- As a third step, the *Parisotoma notabilis* follows. As it is in a more advanced stage of succession, more species find favourable conditions here and are significantly correlated to *P. notabilis*: *Cyphoderus albinus, Entomobrya lanuginosa*, *Entomobrya nivalis*, *Folsomia candida*, *Isotoma anglicana, Isotoma viridis*, *Isotomodes productus, Lepidocyrtus lanuginosus*, *Neanura muscorum* and *Proisotoma minima*. As already said *I. productus* leads over from a *P. minuta* community that has overcome the second stage. This third community in succession is found at sites with dense vegetation, shrub land and the oldest forest sites on reclaimed land. It seems to cover quite a wide range of soil properties. But most basic properties seem to be organic matter content (DUNGER et al. 2002) and soil moisture. Of these features it needs more then the previous *M. macrochaeta* community but less wetness than the *P. minuta* community. pH seems irrelevant (PONGE 2000) though VILKAMAA & HUHTA (1986) called *P. notabilis* alcalophilous. There is also a species leading over to the next stage of succession. *Neanura muscorum* is also found in the following community.

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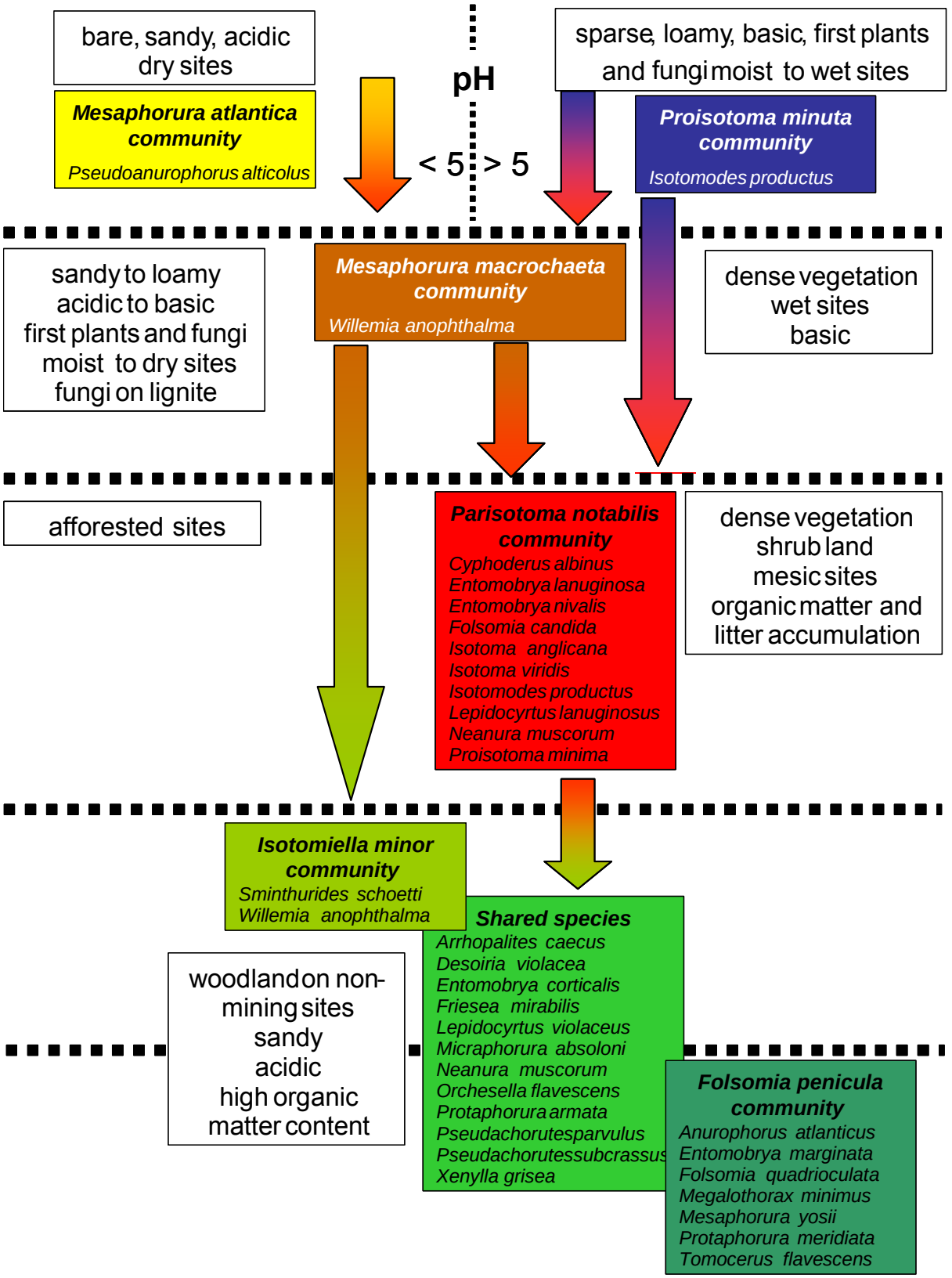

Figure 78: Schematic figure of the communites and their succession. Given are also species significantly correlated to the key-species.

- The next step in succession is somewhat puzzling. There is no clear transition between the previous communities and the following (two?) communities. CASSAGNE (2003) wrote that Isotomidae of the genera *Folsomia* and *Isotomiella* are linked to opposing chemical parameters. That would indicate different communities which cannot be proved by this work's data. But let us try and deal the following *Isotomiella minor* and *Folsomia penicula* communities as two different though closely related communities. They share a number of species: *Arrhopalites caecus*, *Desoria violacea*, *Entomobrya corticalis*, *Friesea mirabilis*, *Lepidocyrtus violaceus*, *Micraphorura absoloni*, *Neanura muscorum*, *Orchesella flavescens*, *Protaphorura armata*, *Pseudachorutes parvulus*, *Pseudachorutes subcrassus* and *Xenylla grisea*. But the *Isotomiella minor* community has as exclusive species *Sminthurides schoetti* and *Willemia anophthalma*, the latter one leading over from the *M. macrochaeta* community. The *Folsomia penicula* community has *Anurophorus atlanticus, Entomobrya marginata, Folsomia quadrioculata*, *Megalothorax minimus, Mesaphorura yosii, Protaphorura meridiata* and *Tomocerus flavescens* as exclusive species. Both communities are linked to the *P. notabilis* community by *Neanura muscorum*.

The *I. minor* community is present at the oldest reference site in Altsorgefeld and should therefore be some kind of climax community. But it has less species richness than the *F. penicula* community which is more diverse. In addition, *I. minor* itself is considered by some authors not as forest species but as acidophilous (VILKAMAA & HUHTA 1986, significant negative correlation to pH in this work) ubiquist species (HAGVAR 1982, SLAWSKI & SLAWSKA 2000, DUNGER 2001, KOVÁC et al. 2001) and *W. anophthalma* is an acidophilous (GISIN1943, HAYBACH 1959, VILKAMAA & HUTHA 1986, PARSON & PARKINSON 1986, HAGVAR & ABRAHMSEN 1984, PONGE 1993, 2000) ubiquist (HAGVAR 1982, RUSEK 1995).

The *F. penicula* community with its exclusive species is made up by stricter forest species. *F. penicula* (DUNGER 2001), *Anurophorus atlanticus* (FJELLBERG 1980, RUSEK 1995), *Entomobrya marginata* (FJELLBERG 1980, DUNGER 1997), *Megalothorax minimus* (SLAWSKA 1997, STERZYNSKA & KUZNETSOVA 1997, CASSAGNE 2004), *Mesaphorura yosii* (DUNGER 1994, FJELLBERG 1998) and *Tomocerus flavescens* (TAMM 1986, DUNGER 1989, 1997) are generally known as acidophilous forest species.

It has already been shown, that the communities in succession are from open habitats to ubiquists and only then to forest species. *Isotomiella minor* and *Parisotoma notabilis* were the dominating species in a spruce forest (KUZNETSOVA, in press), forming a eurotopic community. So the *I. minor* community could be the transition from eurotopic, ubiquist community to stenotopic, acidic forest community. Therefore may be concluded, that the *I. minor* community represents the fourth stage in succession and the *F. penicula* community the most advanced, maybe even climax, stage in succession.

So succession of communities and species seems sufficiently explained. But what does separate the communities? Communities of early successional species are replaced by a denser and richer community of generalists. This is interpreted as the improvement of soil conditions by SHAW (2003). For both pioneer species it was easy to separate them as they are both linked to opposed pH values and pH 5 has been noted as landmark between 2 distinct types of Collembola communities in forests (PONGE et al. 2003). But what distinguishes *M. atlantica* from *M. macrochaeta*? Low pH between 2.9 and 5.0 seems most important to *M. atlantica* but *M. macrochaeta*

dominates sites with a wide range of pH from 4.0 to 7.3. Successes of pioneer species during early stages of succession may be due to preference to the changed environmental conditions or tolerant combined with release of competition or predation pressure (PETERSEN 1995). Sites without melioration and low pH show only sparse vegetation with few *Calamagrostis*-plants and also only few Collembola are found (DUNGER 1991). So competition should be a neglectable factor here although PARR (1979) saw highly competitive species leading to the exclusion of many pioneer species.

WANNER & DUNGER (1999) underlined the importance of protists as primary colonisers in mine soils which seem to be quite independent from pH as only low correlations were found. DUNGER et al. (2002) studied sites near Berzdorf with no obvious unfavourable physical-chemical factors for Collembola. Still a succession of different species was observed. It is suggested that the most important limiting factor there may be food requirement. 1st stage colonisers may be less demanding on food resources, e.g. feed on early accessible food like protozoans. More demanding species establish after the availability of fungi (DUNGER et al. 2002). So food may be the main limiting factor (HAGVAR 1982b). “Bottom up” control of community diversity by changes in the resource base seems to be the rule in terrestrial ecosystems (CHAUVAT et al. 2003), but results of different studies often appear contradictory (CORTE et al. 2003) and control of food chains might also be ”top-down”. However, STILING & ROSSI (1997) argue that in low productive ecosystem as the PML the control of communities is “bottom up”. So food for Collembola must be a key-parameter for succession.

Most collembolan species are dependent on plant cover. Scattered early successional plants act both as shelters against the extreme microclimatic conditions of the non-vegetated soil and as primary food source (PETERSEN 1995). Without hardly any plants at the bare sites, plants and accompanying fungi as main food source must be excluded.

Considering these hypotheses, *M. atlantica* may be indeed living on protozoans or bacteria, which are early available. *M. macrochaeta* seems to be a more demanding species as it comes in a later stage of succession. NIKLASSON et al. (2000) state that *M. macrochaeta* feeds on microorganisms, mainly bacteria, but CORTET et al. (2003) confirms that this species is usually considered as fungal species. So fungi might be additionally or exclusively its food source and therefore it occurs only at sites that provide the conditions for the growth of fungi. This seems easy to understand at sites with sparse or dense vegetation. **Koy-bar-54**, however, is a site without vegetation. What is *M. macrochaeta* living on here? Many sites in the PML contain quite large amounts of lignite. HOHENSEE (pers. comment) found in her work that the remaining lignite on reclamation sites is colonised by e-strain mycorrhiza fungi, at least if the lignite suffered some weathering. In experiment, the e-strain amplitude for pH ranges from 3 to 8. Considering environmental stress like heat and drought, optimal pH for the growth of fungi would be certainly higher than 3 (HOHENSEE, pers. comment). The e-strain amplitude for pH covers the range of pH that *M. macrochaeta* was found at.

So at sites with a rich flora of fungi on lignite, conditions are favourable for *M. macrochaeta* despite the lack of vegetation. This seems to be the case with **koy-bar-54** with a mean loss on ignition of 4.5 % which is about as much as at the 23-year-old red oak afforestation **sch-oak-23**. At **sch-bar-4** there is also remaining lignite in the soil but less than at the previous site (1.7 %). Yet, there was probably not enough time to build up an abundant fungi flora for *M. macrochaeta* to become eudominant and pH of 3.5 is below the optimum. At **ple-bar-59**, pH is more moderate (4.5) but

the soil is almost without organic matter (0.9 %) which could be colonised by fungi and therefore, *M. macrochaeta* is missing. At less acidic afforested sites without herb layer, both species find favourable conditions. Although species richness of trees correlated positively with the density of fungal feeders (HASEGAWA et al. in press) only few pines on almost bare sand would have a limited number of fungal feeders. So *M. macrochaeta* can already feed on the mycorrhiza fungi and becomes eudominant, but without herb layer and all over root penetration, there are still enough microhabitats for *M. atlantica*.

Success of *M. atlantica* and *Proisotoma minuta* as pioneer species are due to preference to different food sources, pH and moisture conditions, combined with release of competition and predation pressure (PETERSEN 1995). *P. minuta* is known to be fungivorous, same as *M. macrochaeta*, but various microbivorous species have different feeding preferences for particular fungi (e.g. THIMM & LARINK 1995, DUNGER 2001, CORTET 2003, NAKAMORI & SIZUKI 2005). Even closely related Collembola species have totally different food preferences (CHEN et al. 1995). Thus, succession of fungi under different moisture conditions in combination with feeding preferences might explain succession of the fungivorous species *P. minuta*, *M. macrochaeta* and *Parisotoma notabilis*.

But soil moisture may not only indirectly influence the collembolan community by the presence or absence of certain fungi. It may also directly influence Collembola. JOOSE (1981) demonstrated that by the examples of *Orchesella cincta* and *Tomocerus minor* that closely related forest communities may be distinguished by the desiccation resistance of the dominant species. Already slight adoptions in moisture can influence locomotion and thereby survival rate under predation. Moreover, loamy or even slurry soils with *P. minuta* (DUNGER 2001) are certainly less aired than dry, sandy soils where *Mesaphorura macrochaeta* is generally found (FJELLBERG 1998). So there are many possible influences on the succession of species and communities which will have to be studied deeper in the future.

These results may not be totally comparable with DUNGER'S works, because soil in the Berzdorf area is not highly contaminated by pyrite like the Lower Lusatia mining area. Sulphur acidification like in Lower Lusatia is not typical for the Berzdorf opencast district (DUNGER 2001). And although mining sites at Böhlen (Leipzig, Saxony) were also heaped with acidic Tertiary sand, they are dominated by species which were not found in this study like *Orchesella quinquefasiciata* and *Hypogastrura vernalis* (ZERLING 1990). So there must be more to regional development of collembolan community than differences in soil quality as DUNGER et al. (2004) postulate. In their study carried out in more neutral sandy soils, *Lepidocyrtus paradoxus* and *Ceratophysella succinea* were dominate, whereas they are hardly relevant in Lower Lusatia.

5.6 Succession of life forms

At the level of species richness, both life forms are significantly positively correlated to structure, organic matter content, water content, water capacity, ammonium and nitrate. To phosphate only endogaeic species are significantly positively correlated. For epigaeic species there is just a tendency to be found at older sites, but for endogaeic species there is a significant positive correlation. For conductivity it is different: Endogaeic species show just a positive tendency, but epigaeic species are significantly positively correlated to conductivity. The positive correlation to organic matter content confirms the results of STANTON (1979) who found that an increase in litter accumulation corresponds to an increase in microarthropod abundance and species richness. He states that this increase would be more pronounced in habitats protected from extreme climatic conditions, which is not the case in the PML.

If we look at the level of dominance of specimens, the picture we see is different. Now there are completely different significances and tendencies. Endogaeic specimens are significantly positively correlated to structure, organic matter content, water content, water capacity and ammonium. Epigaeic specimens have a significantly negative correlation to these parameters. Endogaeic specimens show a tendency to be found at sites with low pH, epigaeic show a tendency to prefer sites with higher pH.

Although soil might be considered as a relatively stable environment, the surface layers are subject to large fluctuations in moisture and temperature (ROCHFEORT 2006). Below-ground communities are influenced to a greater extend by soil properties, whereas above ground communities are influenced by vegetation (DUNGER 1989, CASSAGNET 2003). There is an indirect relationship between plant and soil communities; studies have demonstrated that the distribution of edaphic arthropods is not random but aggregate, following trophic resources and soil moisture (MIGLIORINI et al. 2003).

Epigaeic communities are more influenced by structure, hence the development of vegetation, than endogaeic communities. This is reflected by the fact that the epigaeic community is significantly positively correlated to structure whereas there is a significantly negative correlation for the endogaeic community. Changes in endogaeic communities take longer and these communities are more stable (DUNGER 1989). CASSAGNET (2003) also stresses the influence of vegetation on above ground communities in this context. With the development of dense vegetation, the dominance of epigaeic specimens increases significantly. At sites with dense *Calamagrostis epigejos* vegetation, 62 % of the coverage may be to litter (JAKOB et al. 1996) and therefore an important habitat for epigaeic species. Absence of litter leads to an absence of epigaeic species (PONGE et al. 1993). Epigaeic Collembola do not feed on litter itself but rather on algae, pollen, mineral, faecal and fungal material mixed with bacteria (PONGE 1991, PONGE et al. 1993). KOVÁC et al. (2004) also found that reafforestation generally leads to an increase of edaphic species populations, probably for the lack of a diverse herb and therefore litter layer.

If we now look at the afforestation chronosequence at the changing dominances of specimens, we see differences to foresaid statement of DUNGER (1989). CHAUVAT et al. (2003) found that the early phase of forest rotation was characterised by surface-orientated Collembola whereas the intermediate stages were dominated by euedaphic species. The decrease of the epigaeic Collembola community is probably due to the loss of suitable sources associated with the accumulation of recalcitrant

soil organic matter. Similar results were found in this work (figure 42): Epigaeic specimens decrease after canopy closure. In the afforestation chronosequence they reach highest abundances at the oldest reference site with its heterogeneous canopy. The absence of dense herb layers is caused by canopy closure in stands of intermediate age and results in the lack of a diverse litter layer and therefore the lack of habitat for many epigaeic specimens. Litter now does no longer consist of various herbs (and therefore a diverse microflora) but generally of the dominating tree leaf litter with a smaller variety of microflora. MIGLIORINI et al. (2003) also found such an indirect relationship between plant communities and soil communities. There are subtle edaphic factors which affect the nature of plant community, but not that of the micro-arthropod community. In small "islands" of vegetation of different successional development, the effect of immigration and competitive exclusion by surrounding populations may be the primary determinants of animal community structure (PARR 1979). Diversity within a patch depends on the structure of the surrounding landscape (DAUBER et al. 2003).

Again the littoral site **sch-den-8** is a fine example for different development of the epigaeic and endogaeic communities.

Subsamples A, C, E are immediate to the lake shore, B, D and F three meters further away. With distance the dominances of ecological groups changes in the epigaeic community markedly. At the lake shore, 41.7 % of specimens are of hygrophilous species and 54.5 % specimens of meadow species. Only three meters away from the water dominance of hygrophilous specimens decreases to less than 17 % whereas specimens of meadow species increases to more than 80 % (Figure 63).

The epigaeic community changes far less. There are only specimens of eurotopic species and of meadow species. Dominance of ubiquist specimens increases from 85.3 % to 92.3 % (fig. 79).

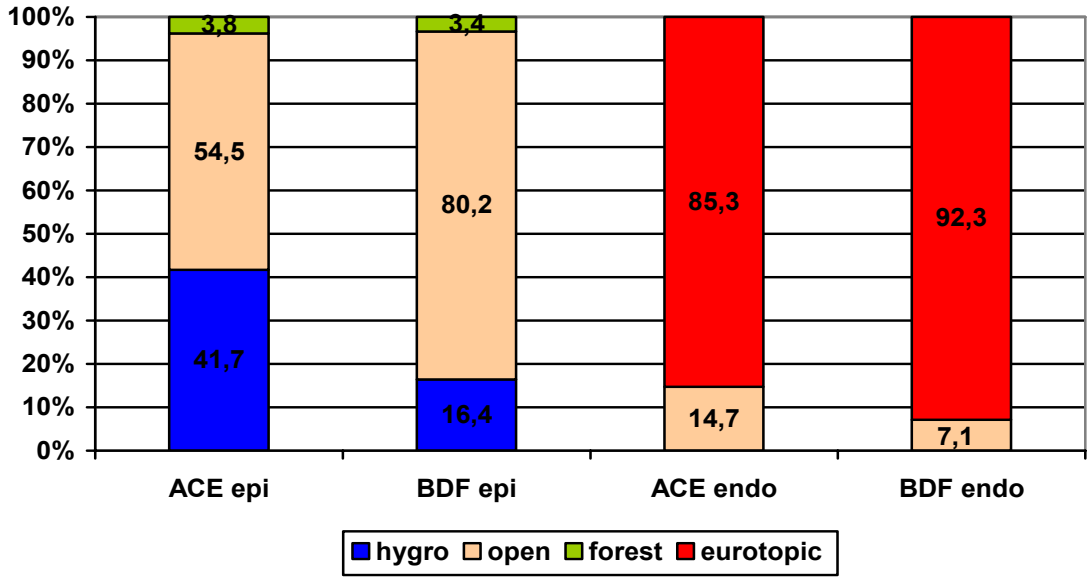

Figure 79: Differences of epigaeic and endogaeic communities and small scale changes at the littoral site.

Some soil parameters change from the subsamples at the lake shore to the other subsamples: conductivity (120.2 to 82.3), water content (19.1 % to 13.8 %), ammonium (0.64 µg/g to 0.40 µg/g) and nitrate (0.84 µg/g to 0.60 µg/g). But the others are quite the same. There is a change within the endogaeic community, but it is not visible at the level of ecological groups. The change is on the level of species and specimens. Both groups of subsamples are dominated by eurotopic species. But the subsambles A, C and E are dominated by *Proisotoma minuta* to 52.9 % whereas the subsamples B, D and F are dominated by *Parisotoma notabilis* to 92.3 %. *Proisotoma minuta* is missing here completely. So here we find some small scale changes in endogaeic communities on the lower levels of species and specimens but hardly on the level of ecological groups.

It was postulated that below-ground communities need more time to build up than those of the above-ground stratum (DUNGER 1989, DUNGER et al. 2002). KUZNETSOVA (in press) supposes that a constant organization of collembolan communities through time arises as a result of successional changes over long periods with relatively stable conditions, allowing the gradual formation of complexes of dominant species. Thus, endogaeic species in succession in the PML are less affected by species turnover than epigaeic species as endogaeic conditions are more stable. The below-ground stratum is more stable and does not suffer as much influence as the above-ground stratum. But thinking of the littoral site in this work, it is still questionable, if the edaphic communities are really that stable and at which community level and site scale do we look?

It is also possible that highly mobile, epedaphic springtails are not viable indicators of soil disturbance as they may constantly invade the study sites (REBEK et al. 2002, CHAUVAT et al. 2003). More sessile, euedaphic species may hold greater potential as biological indicators (REBEK et al. 2002). The fact, that both cluster trees for collembolan communities in this work can be explained by comparing the edaphic communities, seems to underline these statements.

5.7 Conclusions

SCHAAF et al. (1999) conclude that ecosystems on lignite and pyrite containing substrates are dominated by substrate induced processes for many decades. Even after more than 50 years the sites show strong quantitative and qualitative differences in the water and element fluxes compared to non-mine sites. Recovery of collembolan populations may last decades or centuries, depending on dispersal capabilities of the species, proximity of possible sources for the immigration of better adapted species, and absence of a new shift in land use during the meantime (PONGE et al. 2003). Rapid afforestation of open habitats (even on otherwise undisturbed soils) is detrimental for the development of better adapted soil animal communities (PONGE et al. 2003).

DUNGER's mine sites consisted mainly of Pleistocene and Tertiary sands, interspersed with lignite and dark Tertiary loam and clay (DUNGER et al. 2004). Even after fifty years of afforestation, the collembolan community was still markedly different from that of native stands (DUNGER et al. 2004). Reafforestations gained characters very close to those of native forest stands relatively short time (roughly 30 years) after planting (KOVÁC et al. 2004). However, these results are from non-mining sites. Results of DUNGER et al. (2004) can only be stressed by this work. No matter

how old the references sites at Altsorgefeld were (29, 44 or more than a hundred years), the PML is not yet comparable to these stands, at least not on the level of specimens.

SOUSA et al. (in press) stress the importance of native forests for species richness in a fragmented landscape. If these source areas are missing, species diversity declines. Highly disturbed areas as the PML are therefore dependent on surrounding source areas. Older mining sites which where used on a smaller scale should therefore have a greater biodiversity at the same age after reclamation than nowadays vast mining areas.

Processes of primary succession proceed more or less continuously. There are no sharply separated phases of succession, which could be taken as a basis for the description of different steps within the colonization of Collembola (DUNGER et al. 2004). This is definitely true for the epigaeic community which was rather hard to put into a schematic model of succession for lack of statistical evidence. Succession of endogaeic species was far better supported by statistic.

Despite habitat disturbance, a portion of the edaphic community maintains in an ecosystem (CHAUVAT et al. 2003, MIGLIORINI et al. 2003). This distinguishes sites with secondary succession from those in the PML, were no microclimatic niches are occupied by maintaining edaphic species (“first come, first served”).

6. Summary

30 sampling sites at 5 mining areas and reference sites in Lower Lusatia were studied for succession of Collembola. The study took place from 2001 to 2004. Two chronosequences were chosen, one for afforestation sites and one for sites with free succession. Additional data about some soil parameters (pH, organic matter content, water content, water capacity, conductivity, phosphate, ammonium and nitrate) are also given. Most soil parameters increase with age and/or vegetation development. Only pH decreases after melioration whereas no correlations were found for phosphate.

At all study sites, 13.733 specimens, distributed across 84 species were identified with *Mesaphorura macrochaeta* and *Parisotoma notabilis* as most abundant species.

Succession was studied on different levels. On the level of species and ecological groups, succession is from meadow species to forest species, but on the level of specimens and ecological groups, succession is from meadow species over eurotopic species to forest species.

A model for species succession is offered on the level of specimens, presented separately for the epigaeic and the endogaeic community. Both successional developments could be divided into five parts:

For the epigaeic community, the **1st stage** is defined as sites without vegetation. Species found here are *Pseudoanurophorus alticolus, Schoetella ununguiculata, Bourletiella pruinosa* and *Brachystomella parvula*. At the **2nd stage**, already some sparse vegetation can be found. Some sites are also covered densely by moss. Here, *Cryptopygus thermophilus, Isotoma anglicana* and *Lepidocyrtus cyaneus* are found for the first time. The **3rd stage** is defined as sites with dense vegetation, generally *Calamagrostis epigejos* dominated sites. Oldest sites have already some shrubs made of young pines or are clearings in young woodland. Several species are found here for the first time in notable dominances: *Entomobrya lanuginosa, Entomobrya multifasciata, Lepidocyrtus lignorum, Isotoma viridis, Lepidocyrtus lanuginosus, Sminthurinus aureus, Sphaeridia pumilis and Tomocerus flavescens.* The **4th stage** is made up by afforestations up to 43 years on reclamation sites. 5 more species are found here: *Entomobrya nivalis, Neanura muscorum, Orchesella flavescens, Paratullbergia macdougalli* and *Tomocerus vulgaris.* The **5th stage** would be the climax stage, an old oak forest. It is probably not comparable to a true primeval forest, but the type of forest typical for today's mining sites. Only 2 species were found here: *Micraphorura absoloni* and *Entomobrya corticalis***.**

For the endogaeic community, data is even more based on statistical evidence. Succession of the endogaeic community is more dependent on soil parameters and succession of microflora. Generally, succession is from *Mesaphorura atlantica* on acidic sites and *Proisotoma minuta* on sites with higher pH to a *Mesaphorura macrochaeta* community, followed by a *Parisotoma notabilis* dominated community. Older afforested sites are dominated by *Isotomiella minor* and old oak forest on undisturbed sites by *Folsomia penicula*. Duration of the single successional stages depends on parameters like pH, moisture, vegetational structure and availability of certain fungi as basic food resource.

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9. Ecology of Collembola

In the following table, some valuable information from literature is briefly given and statistical results of this work. As the changing dominances of species were tested for correlations, it should be strictly speaking: “The change of dominance of species A is significantly correlated to the change of dominance of species B.” and “The change of dominance of species A is significantly correlated to soil parameter C.” It is the same with the tendencies. We can guess that species with correlated changes in dominance have similar needs and requirements at their environement. For easier reading, foresaid strict language was changed into “Species A is significantly often accompanied by species B” and so on.

Table 43: Some data on the ecology of Collembola.

Anurophorus atlanticus	**forest**		**acidophilous**	**epi**	
	Rare species in moss, under bark, beech-oak forests (FJELLBERG 1980, RUSEK 1995), forest (own results)				
The species is significantly often accompanied by *Arrhopalites caecus* (r = 0.461, p < 0.010), *Entomobrya corticalis* (r = 0.369, p < 0.045), *Folsomia penicula* (r = 0.376, p < 0.041), *Megalothorax minimus* (r =0.597, p < 0.000), *Mesaphorura yosii* (r = 0.597, p < 0.000), *Metaphorura affinis* (r = 0.624, p < 0.000), *Micraphorura absoloni* (r = 0.544, p < 0.002), *Neanura muscorum* (r = 0.401, p < 0.028), *Orchesella flavescens* (r = 0.362, p < 0.049), *Protaphorura armata* (r = 0.553, p < 0.002), *P. meridiata* (r = 0.540, p < 0.002), *Pseudachorutes parvulus* (r = 0.369, p < 0.045), *P. subcrassus* (r = 0.369, p < 0.045), *Sminthurides schoetti* (r = 0.400, p < 0.028), *Tomocerus minor* (0.597, p < 0.000), *Vertagopus arboreus* (r = 0.594, p < 0.001) and *Xenylla grisea* (r = 0.829, p < 0.000). There is a tendency to be found with *Friesea mirabilis* (r = 0.352, p < 0.056) and *Lepidocyrtus violaceus* (r = 0.341, p < 0.065). It has a tendency to be found at structural more developed sites (r = 0.352, p < 0.056), sites with a higher organic matter content (r = 0.352, p < 0.057) and ammonium content (r = 0.353, p < 0.056). It is significantly positively correlated to water capacity (r = 0.376, p < 0.041). It is significantly negatively correlated to pH (r = -0.371, p < 0.044).					
Arrhopalites caecus	**hydrophilous**			**epi**	
	Later stage of succession (ZERLING 1990), muscicolous (MIGLIORINI et al. 2003), hydrophilous (PICHARD et al. 1989), coniferous soils, under stone (FJELLBERG 1980), acido-intolerant (PONGE 2000), rarely reported from mine sites (DUNGER et al. 2004)				
The species is significantly often accompanied by *Anurophorus atlanticus* (r					

= 0.461, p < 0.010), *Desoria violacea* (r = 0.445, p < 0.014), *Entomobrya corticalis* (r = 0.573, p < 0.001), *Folsomia fimetaria* (r = 0.401, p < 0.028), *Folsomia penicula* (r = 0.411, p < 0.024), *Friesea mirabilis* (r = 0.571, p < 0.001), *Isotomiella minor* (r = 0.502, p < 0.005), *Lepidocyrtus violaceus* (r = 0.665, p < 0.000), *Metaphorura affinis* (r = 0.407, p < 0.025), *Micraphorura absoloni* (r = 0.610, p < 0.000), *Orchesella flavescens* (r = 0.398, p < 0.030), *Protaphorura armata* (r = 0.618, p < 0.000), *P. meridiata* (r = 0.401, p < 0.028), *Pseudachorutes parvulus* (r = 0.573, p < 0.001), *Pseudosinella alba* (r = 0.533, p < 0.002), *Sminthurides schoetti* (r = 0.458, p < 0.011), *Tomocerus flavescens* (r = 0.406, p < 0.026), *Xenylla brevicauda* (r = 0.621, p < 0.000) and *Xenylla grisea* (r = 0.597, p < 0.000).

It significantly avoids sites colonized by *Isotoma anglicana* (r = -0.429, p < 0.018).

There is a tendency to be found with *Brachystomella parvula* (r = 0.355, p < 0.071), *Folsomia quadrioculata* (r = 0.351, p < 0.057), *Megalothorax minimus* (r = 0.347, p < 0.060), *Mesaphorura yosii* (r = 0.347, p < 0.060).

It is significantly positively correlated to structure (r = 0.435, p < 0.016), organic matter content (r = 0.571, p < 0.001), conductivity (r = 0.497, p < 0.005), water content (r = 0.433, p < 0.016) and ammonium (r = 0.366, p < 0.046).

There is a tendency to be found at sites with higher water capacity (r = 0.346, p < 0.061).

Bourletiella pruinosa	**open**	**dry**		**epi**	
	1st stage of succession (DUNGER 1975), open, dry habitats (DUNGER 1999), dry meadows (FJELLBERG 1980), confused with *B. hortensis* (FJELLBERG 1980, DUNGER 1999)				

The species is significantly often accompanied by *Brachystomella parvula* (r = 0.531, p < 0.003), *Isotomodes productus* (r = 0.403, p < 0.027) and *Pseudosinella alba* (r = 0.769, p < 0.000).

Brachystomella parvula	**open**	**moist**		**epi**	
	Moist open environments (SZEPTYCKI, 1967, own results), grasslands (CASSAGNAU 1961), 1st stage of succession (DUNGER 1975), young afforestations, epigaeic (DUNGER 1989), open habitats (KOVÁC & MIKLISOVÁ 1997), mesophilous, hemiedaphobiont (RUSEK 1995), wet meadows, disturbed saline soils (FJELLBERG 1982, 1998), youngest soils close to a quarry face (PARR 1978), rapid colonisation after fire (SHAW 1997), “early” species (PARR 1979), meadow species (STERZYNSKA & KUZNETSOVA 1997), lawns, pH 6.5 and 6.9 (ROCHEFORT et al. 2006)				

The species is significantly often accompanied by *Bourletiella pruinosa* (r = 0.531, p < 0.003), *Pseudosinella alba* (r = 0.580, p < 0.001) and *Xenylla*

brevicauda (r = 0.407, p < 0.026). It significantly avoids sites colonized by *Entomobrya nivalis* (r = -0.368, p < 0.045). There is a tendency to avoid sites colonized by *Folsomia candida* (r = -0.352, p < 0.056) and *Isotomurus palustris* (r = 0.356, p < 0.054). There is a tendency to be found with *Arrhopalites caecus* (r = 0.335, p < 0.071), *Isotomodes productus* (r = 0.328, p < 0.077), *Isotomurus palustris* (r = 0.356, p < 0.054). It has a tendency to avoid sites rich in phosphate (r = -0.353, p < 0.056).					
Ceratophysella denticulata	**forest**	**moist**		**epi**	
	Hemiedaphic (CHAUVAT et al. 2003), mesophilous, epigeont (RUSEK 1995), forest (MIGLIORINI et al. 2003), hygrophilous (PICHARD et al. 1989, CASSAGNE et al. 2004), rich organic litter, humid conditions (FJELLBERG 1998), no significant correlations, probably nitrophilous (STIERHOF 2003)				
The species is significantly often accompanied by *Ceratophysella succinea* (r = 0.370, p < 0.044). For this species there is a tendency to be found with *Mesaphorura krausbaueri* (r = 0.341, p < 0.065).					
Ceratophysella succinea	**open**			**epi**	
	Weak in competition (ZERLING 1990), characteristic for earlier stages of succession (DUNGER 1968, 1979), epigaeic (DUNGER 1989), 1st stage of succession (DUNGER 1991, DUNGER et al.2004), eudominant in arable soils (KOVÁC & MIKLISOVÁ 1997, KOVÁC et al. 2001), mesophilous, epigeont (RUSEK 1995), compost species (STERZYNSKA & KUZNETSOVA 1997), probably open habitats, in low abundances (STIERHOF 2003)				
This species is significantly often accompanied by *Ceratophysella denticulata* (r = 0.370, p < 0.044), *Isotomodes productus* (r = 0.369, p< 0.045), *Lepidocyrtus paradoxus* (r = 0.429, p < 0.018), *Mesaphorura krausbaueri* (r = 0.998, p < 0.000), There is a tendency to be found with *Entomobrya multifasciata* (r = 0.335, p < 0.071) and *Tomocerus flavescens* (r = 0.341, p < 0.065). There is a tendency to prefer sites with higher pH values (r =0.352, p < 0.056) and phosphate (r = 0.325, p < 0.080).					
Cryptopygus thermophilus	**open**			**epi**	
	epigaeic (DUNGER 1989), xerothermic, littoral, swamps, hemiedaphobiont (RUSEK 1995), open habitats (PONGE 1993), early				

	successional species on ash sites (SHAW 2003), lawns, pH 6.5 and 6.9 (ROCHEFORT et al. 2006), divers habitats, including open and disturbed forest sites, meadows and others (POPATOV 2001, SOUSA et al. 2004), open habitats (own results)
This species is significantly often accompanied by *Isotomurus palustris* (r = 0.553, p < 0.002), *Mesaphorura hylophila* (r = 0.376, p < 0.041), *Micranurida pygmea* (r = 0.428, p < 0.018), *Willemia aspinata* (r = 0.395, p < 0.031). There is a tendency to be found with *Entomobrya muscorum* (r = 0.343, p < 0.064), *Mesaphorura macrochaeta* (r = 0.332, p < 0.073), *Proisotoma minuta* (r = 0.332, p < 0.073) There is a tendency to be found at sites with higher pH values (r = 0.342, p < 0.064).	
Cyphoderus albinus	**open** | **endo**
	myrmecophilous, mesophilous, euedaphobiont, rocky steppe (RUSEK 1995), grassland (MIGLIORINI et al. 2003), myrmecophilous (STERZYNSKA & KUZNETSOVA 1997, STIERHOF 2003)
The species is significantly often accompanied by *Entomobrya lanuginosus* (r = 0.401, p < 0.028), *Folsomia candida* (r = 0.425, p < 0.019), *Folsomia dovrensis* (r = 0.719, p < 0.000), *Heteromurus nitidus* (r = 0.670, p < 0.000), *Isotoma viridis* (r = 0.515, p < 0.004), *Lepidocyrtus lanuginosus* (r = 0.395, p < 0.031), *L. lignorum* (r = 0.396, p < 0.030), *Mesaphorura hylophila* (r = 0.376, p < 0.041), *Micranurida pygmea* (r = 0.428, p < 9.018), *Parisotoma notabilis* (r = 0.380, p < 0.038), *Proisotoma minima* (r = 0.463, p < 0.010), *Pseudachorutes subcrassus* (r = 0.500, p < 0.005), *Seira domestica* (r = 0.463, p < 0.010) and *Tomocerus flavescens* (r = 0.369, p < 0.045). There is a tendency to be found with *Entomobrya nivalis* (r = 0.354, p < 0.055), *Sminthurides nigromaculatus* (r = 0.340, p < 0.066), It is significantly correlated to ammonium (r = 0.371, p < 0.044). There is a tendency to prefer sites with higher phosphate content (r =0.352, p < 0.057).	
Desoria violacea	**forest** | **epi**
	forest (SLAWSKI & SLAWSKA 2000), mesophilous, epigeont (RUSEK 1995), boreo-montainous (DUNGER 2001), in moss in coniferous forests (FJELLBERG 1980)
The species is significantly often accompanied by *Arrhopalites caecus* (r = 0.445, p < 0.014), *Entomobrya corticalis* (r = 0.831, p < 0.000), *Folsomia candida* (r = 0.366, p < 0.047), *Folsomia fimetaria* (r = 0.425, p < 0.019), *Folsomia penicula* (r = 0.390, p < 0.033), *Folsomia quadrioculata* (r = 0.566, p < 0.001), *Heteromurus nitidus* (r = 515, p < 0.004), *Isotomiella minor* (r = 0.435, p < 0.016), *Lepidocyrtus violaceus* (r = 0.401, p < 0.028), *Megalothorax minimus* (r = 0.556, p < 0.001), *Mesaphorura yosii* (r = 0.556,	

p < 0.001), *Metaphorura affinis* (0.628, p < 0.000), *Micraphorura absoloni* (r = 0.563, p < 0.001), *Orchesella bifasciata* (r = 0.382, p < 0.037), *Orchesella cincta* (r = 0.385, p < 0.036), *Orchesella flavescens* (r = 0.546, p < 0.002), *Protaphorura armata* (r = 0.591, p < 0.001), *Pseudachorutes parvulus* (r = 0.831, p < 0.000), *Tomocerus minor* (r = 0.556, p < 0.001) and *Willemia aspinata* (r = 0.542, p < 0.002), There is a tendency to be found with *Friesea mirabilis* (r = 0.348, p < 0.059), *Pseudachorutes parvulus* (r = 0.341, p < 0.065) and *Xenylla grisea* (r = 0.341, p < 0.065). It is significantly positively correlated to structure (r = 0.352, p < 0.056), organic matter content (r = 0.423, p < 0.020), water content (r = 0.450, p < 0.014), water capacity (r = 0.458, p < 0.011), ammonium (r = 0.509, p < 0.004) and nitrate (r = 0.377, p < 0.048). It is significantly negatively correlated to pH (r = -0.458, p < 0.011).						
Entomobrya corticalis	**forest**				**epi**	
	Under bark on dead trees (FJELLBERG 1980), forest (own results), pH 7.3 (VAN STRAALEN & VERHOEF 1997), tree-climbing (DUNGER 1997)					
The species is significantly often accompanied by *Anurophorus atlanticus* (r = 0.369, p < 0.045), *Arrhopalites caecus* (r = 0.573, p < 0.001), *Desoria violacea* (r = 0.831, p < 0.000), *Folsomia penicula* (r = 0.532, p < 0.002), *F. quadrioculata* (r = 0.707,p < 0.000), *Friesea mirabilis* (r = 0.483, p < 0.007), *Isotomiella minor* (r = 0.462, p < 0.010), *Lepidocyrtus violaceus* (r = 0.500, p < 0.005), *Megalothorax minimus* (r = 0.670, p < 0.000), *Mesaphorura yosii* (r = 0.670, p < 0.000), *Metaphorura affinis* (r = 0.771, p < 0.000), *Micraphorura absoloni* (r = 0.703, p < 0.000), *Orchesella flavescens* (r = 0.458, p < 0.011), *Protaphorura armata* (r = 0.002), *Pseudachorutes parvulus* (r = 1.000, p -), *P. subcrassus* (r = 0.429, p < 0.018) *Tomocerus flavescens* (r = 0.670, p < 0.000) *Willemia anophthalma* (r = 0.443, p < 0.014) and *Xenylla grisea* (r = 0.429, p < 0.018). It is significantly positively correlated to structure (r = 0.423, p < 0.017), organic matter content (r = 0.416, p < 0.022), water content (r = 0.406, p < 0.029), water capacity (r = 0.416, p < 0.022) and ammonium (r = 0.433, p < 0.017). It is significantly negatively correlated to pH (r =-0.408, p < 0.025).						
Entomobrya lanuginosa	**open**				**epi**	
	1st stage of succession (DUNGER 1975, 1989, 1991), initial stages of vegetation at the alpine level (NOSEK 1967), meadows (FJELLBERG 1980)					
This species is significantly often found with *Cyphoderus albinus* (r = 0.401, p < 0.028), *Folsomia dovrensis* (r = 0.597, p < 0.000), *Hypogastrura manubrialis* (r = 0.515, p < 0.004), *Neanura muscorum* (r = 0.441, p < 0.015), *Orchesella villosa* (r = 0.370, p < 0.044), *Parisotoma notabilis* (r = 0.440, p < 0.015), *Proisotoma minima* (r = 0.369, p < 0.045), *Pseudachorutes subcrassus* (r = 0.401, p < 0.028) and *Seira domestica* (r = 0.798, p < 0.000).						

There is a tendency to avoid sites colonized by *Mesaphorura hylophila* (r = -0.342, p < 0.065) and *Micranurida pygmea* (r = -0.325, p <0.080).					
Entomobrya marginata	**open**	**moist**		**epi**	
	mesophilous, macrophytobiont, litoral, swamps (RUSEK 1995), open environments (SZEPTYCKI 1967), in moss on tree trunks, under bark (FJELLBERG 1980), xerophil, tree-climbing, sporadic findings in Germany (DUNGER 1997)				
This species is significantly often found with *Folsomia penicula* (r =0.364, p < 0.048), *Lepidocyrtus violaceus* (r = 0.377, p < 0.040) and *Xenylla grisea* (r = 0.402, p < 0.028). It avoids significantly sites which are colonized by *Entomobrya multifasciata* (r = -0.403, p < 0.027). There is a tendency to be found with *Folsomia quadrioculata* (r = 0.334, p < 0.071). It is significantly correlated to structure (r = 0.568, p < 0.001). There is a tendency to be found at sites with low pH (r = -0.331, p < 0.074) and higher nitrate content (r = 0.357, p < 0.063).					
Entomobrya multifasciata	**open**	**dry**		**epi**	
	Dry open environments (SZEPTYCKI, 1967, DUNGER 1991), tertiary coal sandy dumps, epigaeic (DUNGER 1989), open habitats (PONGE 1993, KOVÁC & MIKLISOVÁ 1997, SHAW 2003), early stage of succession after fire (TAMM, 1986), xerothermic, macrophytobiont, oak woods (RUSEK 1995), forest litter and tree trunks (FJELLBERG 1980)				
This species is significantly negatively correlated to *Entomobrya marginata* (r = -0.403, p < 0.027), *Entomobrya marginalis* (r = -0.403, p < 0.027), *Micraphorura absoloni* (r = -0.362, p < 0.049) There is a tendency to be found with *Ceratophysella succinea* (r = 0.335, p < 0.071), *Mesaphorura krausbaueri* (r = 0.325, p < 0.080), *Pseudosinella octopunctata* (r = 0.326, p < 0.079) and *Tomocerus flavescens* (r = 0.341, p < 0.065). There is a tendency to avoid sites colonized by *Folsomia penicula* (r = -0.350, p < 0.058) and *Mesaphorura atlantica* (r = -0.329, p < 0.076).					
Entomobrya muscorum	**forest**			**epi**	own results
This species is significantly often found with *Entomobrya nivalis* (r = 0.500, p < 0.005), *Gisinianus flammeolus* (r = 0.515, p < 0.004), *Lepidocyrtus curvicollis* (r = 0.556, p < 0.001), *L. lanuginosus* (r 0 0.472, p < 0.008), *L. lignorum* (r = 0.442, p < 0.015), *Orchesella cincta* (r = 0.486, p < 0.006), *Mesaphorura hylophila* (r = 0.368, p < 0.045) and *Willemia anophthalma* (r = 0.636, p < 0.000).					

There is a tendency to be found with *Cryptopygus thermophilus* (r = 0.342, p < 0.064), *Willemia aspinata* (r = 0.340, p < 0.066) and *Willemia intermedia* (r = 0.333, p < 0.073).

There is a tendency to avoid sites colonized by *Mesaphorura critica* (r = -0.341, p < 0.065).

It is significantly correlated to structure (r = 0.380, p < 0.038).

Entomobrya nivalis	**forest**	**dry**		**epi**	
	Early stage of succession after fire (TAMM 1986), corticolous (PONGE 1993, Stierhof 2003), epigaeic, forest (DUNGER 1991, MIGLIORINI et al. 2003), mesophilous, macrophytobiont, beech-oak woods (RUSEK 1995), dry sites (PONGE 1993), usually dry habitats (FJELLBERG 1980), tree-climbing (HOPKINS 1997, DUNGER 1997), "late" species (PARR 1979)				

This species is significantly often found with *Folsomia candida* (r = 0.566, p < 0.001), *Entomobrya muscorum* (r = 0.500, p < 0.005), *Lepidocyrtus lignorum* (r = 0.360, p < 0.050), *Orchesella cincta* (r = 0.505, p < 0.004), *Parisotoma notabilis* (r = 0.363, p < 0.048), *Seira domestica* (r = 0.415, p < 0.022), *Sminthurus nigromaculatus* (r = 0.467, p < 0.009) and *Willemia anophthalma* (r = 0.434, p < 0.016).

It is significantly negatively correlated to *Brachystomella parvula* (r = -0.368, p < 0.045).

There is a tendency to be found with *Cyphoderus albinus* (r = 0.354, p < 0.055), *Folsomia dovrensis* (r = 0.351, p < 0.057), and *Isotoma viridis* (r = 0.333, p < 0.072).

It is significantly correlated to structure (r = 0.469, p < 0.009), water content (r = 0.391, p < 0.036), water capacity (r = 0.420, p < 0.021) and ammonium (r = 0.392, p < 0.032).

Folsomia candida	**ubiquist**			**endo**	
	Later stage of succession (ZERLING 1990), thermophilous, ruderal and troglophilous species, not common in strongly disturbed areas (DUNGER 2001), more often in slightly disturbed habitats than in natural sites, probably thermophilous, prefers sites rich in nutrition (STIERHOF 2003), pH 5.6 (VAN STRAALEN & VERHOEF 1997), regular inhabitant of mine-dump soils (DUNGER et al. 2002), frequent in compost (FJELLBERG 1980), lawns, pH 6.5 and 6.9 (ROCHEFORT et al. 2006)				

This species is significantly often found with *Cyphoderus albinus* (r = 0.425, p < 0.019), *Desoria violacea* (r = 0.366, p < 0.047), *Entomobrya nivalis* (r = 0.566, p < 0.001), *Folsomia fimetaria* (r = 0.510, p < 0.004), *Mesaphorura italica* (r = 0.372, p < 0.043), *Orchesella flavescens* (r = 0.384, p < 0.036),

Parisotoma notabilis (r = 0.426, p < 0.019) *Seira domestica* (r = 0.396, p < 0.030)*, Sminthurus viridis* (r = 0.372, p < 0.043), *Sphaeridia pumilis* (r = 0.375, p < 0.041) and *Willemia anophthalma* (r = 0.365, p < 0.047).

It is significantly negatively correlated to *Schoetella ununguiculata* (r = -0.381, p < 0.038).

There is a tendency to avoid sites colonized by *Brachystomella parvula* (r = -0.352, p < 0.056).

It is significantly correlated to organic matter content (r = 0.385, p < 0.035), water content (r = 0.447, p < 0.015), water capacity (r = 0.453, p < 0.012), phosphate (r = 0.487, p < 0.006) and ammonium (r = 0.577, p < 0.001).

There is a tendency to appear in older sites (r = 0.331, p < 0.074) with better developed vegetation structure (r = 0.326, p < 0.079).

Folsomia dovrensis	**forest**	**dry**		**endo**	
	Rare species of dryer forests and meadows (DUNGER 2001), coniferous soils (FJELLBERG 1980), first recorded for Germany				

This species is significantly often found with *Cyphoderus albinus* (r = 0.719, p < 0.000), *Entomobrya lanuginosa* (r = 0.597, p < 0.000), *Neanura muscorum* (r = 0.384, p < 0.036), *Proisotoma minima* (r = 0.670, p < 0.000), *Pseudachorutes subcrassus* (r = 0.719, p < 0.000), *Seira domestica* (r = 0.670, p < 0.000), *Sminthurus nigromaculatus* (r = 0.515, p < 0.004) and *Vertagopus arboreus* (r = 0.391, p < 0.033).

There is a tendency to be found with *Entomobrya nivalis* (r = 0.351, p < 0.057), *Isotoma viridis* (r = 0.345, p < 0.062) and *Lepidocyrtus lignorum* (r = 0.335, p < 0.070).

Folsomia fimetaria	**ubiquist**			**endo**	
	Later stage of Succession (ZERLING 1990), nitrophiluos and ruderal species, seldom in forests, characteristic for meadows and soils of farming systems (DUNGER 2001), alcalophilous (VILKAMAA & HUHTA, 1986), ubiquist (KOVÁC et al. 2001), decaying organic substrate (FJELLBERG 1980), ruderal species (STERZYNSKA & KUZNETSOVA 1997)				

This species is significantly often found with *Arrhopalites caecus* (r = 0.401, p < 0.028), *Desoria violacea* (r = 0.425, p < 0.019), *Folsomia candida* (r = 0.510, p < 0.004)*, Heteromurus nitidus* (r = 0.391, p < 0.033), *Lepidocyrtus lanuginosus* (r= 0.399, p < 0.029), *Lepidocyrtus lignorum* (r = 0.365, p < 0.047), *Lepidocyrtus paradoxus* (r = 0.499, p < 0.005), *Orchesella cincta* (r = 0.380, p < 0.038), *Protaphorura armata* (r = 0.464, p < 0.010)*, Pseudosinella alba* (r = 0.416, p < 0.022) *Sphaeridia pumilis* (r = 0.428, p < 0.018), *Tomocerus flavescens* (r = 0.602, p < 0.000), *Willemia anophthalma* (r = 0.401, p < 0.028) and *Xenylla brevicauda* (r = 0.419, p < 0.021).

It is significantly positively correlated to age (0.366, p < 0.047), organic matter content (r = 0.405, p < 0.026) and ammonium (r = 0.416, p < 0.022).

There is a tendency to be found with *Mesaphorura italica* (r = 0.333, p <

0.072), *Sminthurides malmgreni* (r = 0.333, p < 0.072), *Sminthurus viridis* (r = 0.333, p < 0.072) and *Parisotoma notabilis* (r = 0.328, p < 0.077). There is a tendency to be found at sites with more developed vegetation structure (r = 0.351, p < 0.057), higher water content (r = 0.356, p < 0.058).					
Folsomia manolachei	**ubiquist**			**endo**	
	Dryer Forests (PONGE 1993), eurotopic species (DUNGER 2001), pH indifferent (PONGE 2000), dominant under spruce in the Pyrenees (CASSAGNE et al. 2004), not in PML (DUNGER et al. 2004)				
There is a tendency to be found with *Proisotoma minuta* (r = 0.328, p < 0.077). This is a rare species in the PML. It only occurred in just one sampling site.					
Folsomia onychiurina		**dry**		**endo**	
	In eastern Asia in different kind of forests and grassland, prob. artificially introduced species in Europe, psammophilous (DUNGER 2001)				
There is an almost significant tendency to be found with *Lepidocyrtus lignorum* (r = 0.360, p < 0.051). This is a rare species in the PML. It only occurred in just one sampling site.					
Folsomia penicula	**forest**		**acidophilous**	**endo**	
	Mesophilic and mostly forest species with high abundances (DUNGER 2001), prefers acid and humus soils (ZIVADINOVIC et al. 1991), mesophilous, euedaphobiont (RUSEK 1995), forest, acidophilic (own results), acido-intolerant (PONGE 2000)				
This species is significantly often found with *Anurophorus atlanticus* (r = 0.376, p < 0.041), *Arrhopalites caecus* (r = 0.411, p < 0.024), *Desoria violacea* (r = 0.390, p < 0.033), *Entomobrya corticalis* (r = 0.532, p < 0.002), *Entomobrya marginata* (r = 0.364, p < 0.048), *Folsomia quadrioculata* (r = 0.497, p < 0.005), *Friesea mirabilis* (r = 0.745, p < 0.000), *Isotomiella minor* (r = 0.689, p < 0.000), *Lepidocyrtus violaceus* (r = 0.498, p < 0.005), *Megalothorax minimus* (r = 0.384, p < 0.036), *Mesaphorura yosii* (r = 0.384, p < 0.036), *Micraphorura absoloni* (r = 0.690, p < 0.000), *Neanura muscorum* (r = 0.637, p < 0.000), *Orchesella flavescens* (r = 0.618, p < 0.000), *Protaphorura armata* (r = 0.390, p < 0.033), *Protaphorura meridiata* (r = 0.424, p < 0.019), *Pseudachorutes parvulus* (r = 0.532, p < 0.002), *Pseudachorutes subcrassus* (r = 0.493, p < 0.006), *Tomocerus flavescens* (r = 0.384, p < 0.036) and *Xenylla grisea* (r = 0.513, p < 0.004). There is a tendency to avoid sites colonized by *Entomobrya multifasciata* (r = -0.350, p < 0.058), *Metaphorura affinis* (r = 0.351, p < 0.057), *Willemia anophthalma* (r = 0.352, p < 0.056) It is significantly correlated to age (r = 0.392, p < 0.032), structure (r = 0.581, p < 0.001), organic matter content (r = 0.468, p < 0.009), water content (r =					

0.415, p < 0.025), water capacity (r = 0.493, p < 0.006), ammonium (r = 0.486, p < 0.006). There is a tendency to be found at sites with low pH (r = -0.354, p < 0.055).					
Folsomia quadrioculata	**ubiquist**	**moist**		**endo**	
	Hygrophilous (PONGE 1993, KOVÁC et al. 2001), eurotopic litter dwelling species with a moderate preference for damp sites (DUNGER 2001), most abundant in forest sites (PONGE et al. 2003), shrubs (SHAW 2003), hemiedaphic (CHAUVAT et al. 2003), ubiquist (HAGVAR 1982, KOVÁC et al. 2001), eurotopic (FJELLBERG 1980, SLAWSKI & SLAWSKA 2000), mesophilous, euedaphobiont (RUSEK 1995), more advanced stages of succession (RUSEK 2004), hygrophilous (CASSAGNE et al. 2004), not in PML (DUNGER et al. 2004), significantly correlated to organic matter content, soil moisture and phosphate (KOVÁC et al. 2004), forest (own results)				
This species is significantly often found with *Desoria violacea* (r = 0.566, p < 0.001), *Entomobrya corticalis* (r = 0.707, p < 0.000), *Folsomia penicula* (r = 0.497, p < 0.005), *Friesea mirabilis* (r = 0.444, p< 0.014), *Megalothorax minimus* (r = 0.454, p < 0.012), *Mesaphorura yosii* (r = 0.454, p< 0.012), *Metaphorura affinis* (r = 0.521, p < 0.003), *Micraphorura absoloni* (r = 0.457, p < 0.011), *Orchesella flavescens* (r = 0.511, p < 0.004), *Protaphorura armata* (r = 0.512, p < 0.004), *Protaphorura meridiata* (r = 0.418, p < 0.021), *Pseudachorutes parvulus* (r = 0.707, p < 0.000), *Tomocerus minor* (r =0.454, p < 0.012), *Willemia anophthalma* (r = 0.498, p < 0.005) and *Xenylla acauda* (r = 0.456, p < 0.011). There is a tendency to be found with *Arrhopalites caecus* (r = 0.351, p < 0.057), *Entomobrya marginata* (r = 0.334, p < 0.071), *Isotomiella minor* (r = 0.336, p < 0.070), *Lepidocyrtus violaceus* (r = 0.341, p < 0.065), *Orchesella cincta* (r = 0.350, p < 0.058). It is significantly positively correlated to structure (r = 0.506, p < 0.004). There is a tendency to be found at sites with higher organic matter content (r = 0.328, p < 0.077) and ammonium content (r = 0.325, p < 0.079). The species was not found in the successional chronosequence.					
Friesea mirabilis	**ubiquist**			**endo**	
	Acediphob (HAGVAR & ABRAHAMSEN, 1984), acidophilious (GISIN 1943, HAYBACH 1959, PONGE 1993, PONGE 2000), later stage of succession after fire, ubiquist (TAMM 1986), euedaphic (DUNGER 1991), predator (DUNGER 1997), avoids only the driest sites (FJELLBERG 1998), typical for coniferous forest (HAGVAR 1982), woodland on ash soil (SHAW 2003), climax phase [pine forest] in				

	dune succession (SLAWSKA 1997), most advanced stages of succession, connected to aquatic soil microfauna (RUSEK 2004), prefers spruce over beech forest (CASSAGNE et al. 2004), in larger woodlands (STIERHOF 2003), forest (own results)

This species is significantly often found with *Arrhopalites caecus* (r = 0.571, p < 0.001), *Entomobrya corticalis* (r = 0.483, p < 0.007), *Folsomia penicula* (r = 0.745, p < 0.000)*, Folsomia quadrioculata* (r = 0.444, p < 0.014)*, Isotomiella minor* (r = 0.798, p < 0.000), *Lepidocyrtus violaceus* (r = 0.419, p < 0.021), *Megalothorax minimus* (r = 0.384, p < 0.036), *Mesaphorura yosii* (r = 0.384, p < 0.036), *Micraphorura absoloni* (r = 0.443, p < 0.014), *Neanura muscorum* (r = 0.627, p < 0.000), *Orchesella bifasciata* (r = 0.409, p < 0.025), *Orchesella flavescens* (r = 0.620, p < 0.000), *Protaphorura armata* (r = 0.543, p < 0.002), *Pseudachorutes parvulus* (r = 0.483, p < 0.007), *Pseudachorutes subcrassus* (r = 0.434, p < 0.017), *Sminthurus schoetti* (r = 0.414, p < 0.023), *Tomocerus minor* (r = 0.384, p < 0.036), *Xenylla acauda* (r = 0.370, p < 0.044), *Xenylla grisea* (r = 0.483, p < 0.007)*.*

There is a tendency to be found with *Anurophorus atlanticus* (r = 0.352, p < 0.056), *Desoria violacea* (r = 0.348, p < 0.059), *Lepidocyrtus lignorum* (r = 0.326, p < 0.079), *Protaphorura meridiata* (r = 0.357, p < 0.053) and *Vertagopus arboreus* (r = 0.358, p < 0.052)*.*

There is a tendency to avoid sites colonized by *Mesaphorura atlantica* (r = -0.344, p < 0.063)*, M. critica* and *M. hylophila*.

It is significantly positively correlated to age (r = 0.418, p < 0.022), structure (r = 0.690, p < 0.000), organic matter content (r = 0.652, p < 0.000), conductivity (r = 0.374, p < 0.042), water content (r = 0.427, p < 0.021), water capacity (r = 0.557, p < 0.001) and ammonium (r = 0.437, p < 0.016).

There is a tendency to be found at sites with higher nitrate content (r = 0.352, p < 0.066).

Gisinianus flammeolus	**forest**			**epi**	
	Wet and dry litter, moss, rotten wood, not abundant (DUNGER 1999), deciduous forest litter (FJELLBERG 1980)				

This species is significantly often found with *Entomobrya muscorum* (r = 0.515, p < 0.004), *Willemia aspinata* (r = 0.719, p < 0.000).

There is a tendency to be found with *Micraphorura pygmea* (r = 0.328, p < 0.076), *Willemia anophthalma* (r = 0.345, p < 0.062) and *Sminthurinus aureus* (r = 0.328, p < 0.077).

Heteromurus nitidus	**hygrophilous**		**acidintolerant**	**endo**	
	mesophilous, euedaphobiont (RUSEK 1995), hygrophilous (MIGLIORINI et al. 2003), frequent in deep soil (FJELLBERG 1980), eumull (PONGE et al. 2003), acido-intolerant (PONGE 2000)				

This species is significantly often found *Cyphoderus albinus* (r = 0.670, p <

0.000), *Desoiria violacea* (r = 0.515, p < 0.004), *Folsomia fimetaria* (r = 0.391, p < 0.033), *Isotoma viridis* (r = 0.372, p < 0.043), *Microanurophorus musci* (r = 0.369, p < 0.045), *Orchesella bifasciata* (r = 0.445, p < 0.014), *Orchesella cincta* (r = 0.413, p< 0.023), *Tomocerus flavescens* (r = 0.597, p < 0.000).					
Hypogastrura manubrialis	**ubiquist**			**endo**	
	Compost and other organic deposits (LINNANIEMI 1912), wet open site, early successional species on ash sites (SHAW 2003), young disturbed habitats (SHAW 2003), co-dominant on youngest mine spoil sites (PARSONS & PARKINSON 1986), fungivorous (NAKAMORI & SUZUKI 2005)				
This species is significantly often found with *Entomobrya lanuginosa* (r = 0.515, p < 0.004), *Isotomodes productus* (r = 0.515, p < 0.004) and *Seira domestica* (r = 0.719, p < 0.000), *Sminthurides schoetti* (r = 0.414, p < 0.023).					
Isotoma anglicana	**open**	**dry**		**epi**	
	1st stage of succession, r-strategist (ZERLING 1990), eurotopic species with a high preference for open biotops (DUNGER 2001), grassland, algivorous (RUSEK 1989), open areas (SLAWSKI & SLAWSKA 2000), mesophilous, epigeont (RUSEK 1995)				
This species is significantly often found with *Parisotoma notabilis* (r = 0.387, p < 0.035). It is significantly negatively correlated to *Arrhopalites caecus* (r = -0.429, p < 0.018). There is a tendency to be found with *Seira domestica* (r = 0.348, p < 0.060). There is a tendency to avoid sites colonized by *Orchesella villosa* (r = -0.328, p < 0.076) and *Xenylla grisea* (r = -0.328, p < 0.076), *Paratullbergia macdougalli* (r = 0.354, p < 0.055).					
Isotoma viridis	**open**	**moist**		**epi**	
	Moist open environments (SZEPTYCKI 1967), feeds on fungal hyphae and decaying leaf matter, but may also prey on other microarthropods (POOLE 1959), on loamy or sandy Pleistocene dumps, epigaeic (DUNGER 1989), eurotopic species with a high preference for open sites, epigeic (DUNGER 2001), 1st stage (DUNGER 1991), later stage of succession after fire (TAMM 1986), algivorous (RUSEK 1992), open areas (SLAWSKI & SLAWSKA 2000), drift exposed (DUNGER et al. 2002), beech-oak forest, mesophilous, epigeont (RUSEK 1995), common in various habitats (FJELLBERG				

	1980), open habitats (PONGE et al. 2003), largest part of biomass on newly reclaimed coal shales (PARSONS & PARKINSON 1986), meadow species (STERZYNSKA & KUZNETSOVA 1997), abundant in meadows and agricultural sites (POPATOV 2001), rarely in forests (STIERHOF 2003), lawns, pH 6.5 and 6.9 (ROCHEFORT et al. 2006)
This species is significantly often found with *Cyphoderus albinus* (r = 0.515, p < 0.004), *Heteromurus nitidus* (r = 0.372, p < 0.043), *Isotomodes productus* (r = 0.509, p < 0.004), *Lepidocyrtus lanuginosus* (r = 0.366, p < 0.046), *Lepidocyrtus lignorum* (r = 0.405, p < 0.026), *Paratullbergia macdougalli* (r = 0.422, p < 0.020), *Parisotoma notabilis* (r = 0.531, p < 0.003), *Proisotoma minima* (r = 0.403, p < 0.027), *Sminthurides schoetti* (r = 0.418, p < 0.021), *Seira domestica* (r = 0.403, p < 0.027), *Sphaeridia pumilis* (r = 0.419, p < 0.021) and *Tomocerus flavescens* (r = 0.622, p < 0.000). There is a tendency to be found with *Entomobrya nivalis* (r = 0.333, p < 0.072), *Folsomia dovrensis* (r = 0.345, p < 0.062), *Proisotoma minuta* (r = 0.337, p < 0.069), *Sminthurus nigromaculatus* (r = 0.328, p < 0.077)	
Isotomiella minor	**forest** | **acidophilous** | **endo**
	Generalist (HAGVAR 1982), ubiquist (KOVÁC et al. 2001), eurotopic litter-dwelling species with high abundances and a moderate preference for wet and forest sites (DUNGER 2001), dominant in spruce forests (PFLUG & WOLTERS 2002), later stage of Succession (ZERLING 1990), euedaphic (DUNGER 1991, CHAUVAT et al. 2003), acidophilous (VILKAMAA & HUHTA 1986), pH indifferent (PONGE 2000), parthenogenic (PETERSEN 1978), forest (RUSEK 1989, KUZNETSOVA 2003), eurotopic (SLAWSKI & SLAWSKA 2000), forest (JUCEVICA & MELCIS 2002), mesophilous, euedaphobiont (RUSEK 1995), typical for coniferous forest (HAGVAR 1982), forest (STERZYNSKA & KUZNETSOVA 1997), most advanced stages of succession (RUSEK 2004), prevail in oak forests (KOVAC et al. 2005), lawns, pH 6.5 and 6.9 (ROCHEFORt et al. 2006), dominant under beech and spruce (CASSAGNE et al. 2004), significantly correlated to phosphate (KOVÁC et al. 2004), forest (own results)
This species is significantly often found with *Arrhopalites caecus* (r = 0.502, p < 0.005), *Desoria violacea* (r = 0.435, p < 0.016), *Entomobrya corticalis* (r = 0.462, p < 0.010), *Folsomia penicula* (r = 0.689, p < 0.000)*, Friesea mirabilis* (r = 0.798, p < 0.000), *Lepidocyrtus violaceus* (r = 0.430, p < 0.018), *Micraphorura absoloni* (r = 0.605, p < 0.000), *Neanura muscorum* (r = 0.461, p < 0.010), *Orchesella flavescens* (r = 0.600, p < 0.000), *Protaphorura*	

armata (r = 0.473, p < 0.008), *Pseudachorutes parvulus* (r = 0.462, p < 0.010), *Pseudachorutes subcrassus* (r = 0.376, p < 0.040), *Sminthurides schoetti* (r = 0.395, p < 0.031), *Willemia anophthalma* (r = 0.438, p < 0.015) and *Xenylla grisea* (r = 0.445, p < 0.014). There is a tendency to be found with *Folsomia quadrioculata* (r = 0.336, p < 0.070), *Megalothorax minimus* (r = 0.333, p < 0.072), *Mesaphorura yosii* (r = 0.333, p < 0.072), *Orchesella bifasciata* (r = 0.342, p < 0.064), *Orchesella cincta* (r = 0.347, p < 0.060) and *Tomocerus minor* (r = 0.333, p < 0.072). It is significantly positively correlated to age (r = 0.417, p < 0.022), structure (r = 9.634, p < 0.000), organic matter content (r = 0.565, p < 0.001), water content (r = 0.450, p < 0.014), water capacity (r = 0.625, p < 0.000) and ammonium (r = 0.411, p < 0.024). There is a tendency to be found at sites with higher nitrate content (r = 0.349, p< 0.069). It is significantly negatively correlated to pH (r = -0.371, p < 0.044).					
Isotomodes productus	**open**	**dry**		**endo**	
	Common species in soils of different open, dry sites with low abundance (DUNGER 2001). In East Germany, it was found only in open-dry plots (DUNGER 1984), 2nd stage of succession, K-strategist (DUNGER 1989, ZERLING 1990), euedaphic (DUNGER 1991), open areas (SLAWSKI & SLAWSKA 2000, MIGLIORINI et al. 2003), xerothermic, euedaphobiont (RUSEK 1995), dry, sandy meadows and xerophilic plant communities (FJELLBERG 1980), wooded sites (SHAW 2003), meadow species (STERZYNSKA & KUZNETSOVA 1997), open habitats, thermophilous (STIERHOF 2003), lawns, pH 6.5 and 6.9 (ROCHEFORT et al. 2006)				
This species is significantly often found with *Bourletiella pruinosa* (r = 0.403, p < 0.027), *Ceratophysella succinea* (r = 0.369, p < 0.045), *Hypogastrura manubrialis* (r = 0.515, p < 0.004), *Isotoma viridis* (r = 0.509, p < 0.004), *Isotomurus palustris* (r = 0.461, p < 0.010), *Lepidocyrtus paradoxus* (r = 0.369, p < 0.045), *Mesaphorura krausbaueri* (r = 0.401, p < 0.028), *Paratullbergia macdougalli* (r = 0.387, p < 0.035), *Parisotoma notabilis* (r = 0.389, p < 0.034), *Proisotoma minuta* (r = 0.462, p < 0.010), *Proisotoma minima* (r = 0.370, p < 0.044), *Pseudosinella alba* (r = 0.414, p < 0.023), *Sminthurides schoetti* (r = 0.668, p < 0.000) and *Sphaeridia pumilis* (r = 0.393, p < 0.032). There is a tendency to be found with *Brachystomella parvula* (r = 0.328, p < 0.077), *Seira domestica* (r = 0.340, p < 0.066). It is significantly positively correlated to pH (r = 0.482, p < 0.007), conductivity (r = 0.465, p < 0.010) and phosphate (r = 0.376, p < 0.041).					
Isotomurus palustris	**open**	**moist**		**epi**	

	Moist open environments (SZEPTYCKI 1967), Hygrophilous (PONGE 1993), later stage of succession after fire, r-strategist (TAMM 1986), algivorous (RUSEK 1989, 1992), drift exposed (DUNGER et al. 2002), hygrophilous, epigeont (RUSEK 1995), wet habitats (FJELLBERG 1980), rarely in forests, hygrophilous (STIERHOF 2003), hygrophilous (own results)

This species is significantly often accompanied by *Cryptopygus thermophilus* (r = 0.553, p < 0.002), *Isotomodes productus* (r = 0.461, p < 0.010), *Lepidocyrtus lanuginosus* (r = 0.414, p < 0.023), *Pseudosinella alba* (r = 0.449, p < 0.013) and *Tomocerus flavescens* (r = 0.366, p< 0.046).

There is a tendency to be found with *Brachystomella parvula* (r = 0.356, p < 0.054) and *Tomocerus vulgaris* (r = 0.344, p < 0.062).

It is significantly positively correlated to pH (r = 0.390, p < 0,033).

Lepidocyrtus curvicollis	**forest**	**moist**	**acidintolerant**	**epi**	
	Moist sites, litter and vegetation (FJELLBERG 1980), forest (MIGLIORINI et al. 2003), litter (DUNGER 1997), rare species, acidintolerant (STIERHOF 2003)				

This species is significantly often found with *Entomobrya muscorum* (r = 0.556, p < 0.001).

Lepidocyrtus cyaneus	**open**			**epi**	
	epigaeic, 3rd stage (DUNGER 1989, SHAW 2003), 2nd stage of Succession, open landscapes (ZERLING 1990), dominant in arable soils (KOVÁC & MIKLISOVÁ 1997), bisexual (PETERSEN 1978), species absent for a long time after fire (TAMM 1986), pH 6.6 (VAN STRAALEN & VERHOEF 1997), self-motile (DUNGER et al. 2002), mesophilous, microphytobiont, litoral, swamps (RUSEK 1995), grassland (MIGLIORINI et al. 2003), litter from various plant communities (FJELLBERG 1980), later in succession on ash sites (SHAW 2003), open habitats (STIERHOF 2003)				

This species is significantly often found with *Lepidocyrtus violaceus* (r = 0.391, p < 0.033).

There is a tendency to be found with *Mesaphorura tenuisensillata* (r = 0.345, p < 0.062) and *Protaphorura meridiata* (r = 0.329, p < 0.075).

There is a tendency to avoid sites colonized by *Lepidocyrtus lanuginosus* (r = -0.343, p < 0.063).

It is significantly positively correlated to nitrate (r = 0.388, p < 0.041).

Lepidocyrtus lanuginosus	**forest**			**epi**	
	Epedaphic (CHAUVAT et al. 2003), 1st stage of succession (DUNGER 1991, IRMLER 1996), mesophilous, epigeont, littoral, swamps (RUSEK 1995), forest (MIGLIORINI et al. 2003), compost (FJELLBERG 1980), more advanced stages of succession (RUSEK 2004)				

This species is significantly often found with *Cyphoderus albinus* (r = 0.395, p < 0.031), *Entomobrya muscorum* (r = 0.472, p < 0.008), *Folsomia fimetaria* (r = 0.399, p < 0.029), *Isotomurus palustris* (r = 0.414, p < 0.023), *Isotoma viridis* (r = 0.366, p < 0.046), *Lepidocyrtus lignorum* (r = 0.508, p < 0.004), *Parisotoma notabilis* (r = 0.388, p < 0.034), *Pseudosinella octopunctata* (r = 0.371, p < 0.044) and *Tomocerus flavescens* (r = 0.470, p < 0.009)

It significantly avoids sites colonized by *Mesaphorura atlantica* (r = -0.475, p < 0.008) and *Mesaphorura critica* (r = -0.369, p < 0.044).

There is a tendency to be found at sites colonized by *Orchesella cincta* (r = 0.346, p < 0.061)

There is a tendency to avoid sites colonized by *Lepidocyrtus cyaneus* (r = -0.343, p <0.063), *Pseudoanurophorus alticolus* (r = -0.327, p < 0.078), *Willemia anophthalma* (r = 0.357, p < 0.053).

It is significantly positively correlated to ammonium (r = 0.445, p < 0.014).

There is a tendency to be found at sites with more developed vegetation structure (r = 0.344, p < 0.063).

Lepidocyrtus lignorum	**forest**			**epi**	
	Bisexuell (PETERSEN 1978), grassland (RUSEK 1989), eurotopic (SLAWSKI & SLAWSKA 2000), mesophilous, epigeont (RUSEK 1995), forest (MIGLIORINI et al. 2003), common in various plant communities (FJELLBERG 1980), typical for coniferous forest (HAGVAR 1982), hygrophilous (PONGE et al. 2003), “late” species (PARR 1979) , dry litter (DUNGER 1997)				

This species is significantly often found with *Cyphoderus albinus* (r = 0.396, p < 0.030), *Entomobrya muscorum* (r = 0.442, p < 0.015), *Entomobrya nivalis* (r = 0.360, p < 0.050), *Folsomia fimetaria* (r = 0.365, p < 0.047), *Isotoma viridis* (r = 0.405, p < 0.026), *Lepidocyrtus lanuginosus* (r = 0.508, p < 0.004), *Orchesella cincta* (r = 0.437, p < 0.016) and *Tomocerus flavescens* (r = 0.396, p < 0.030).

There is a tendency to be found with *Folsomia dovrensis* (r = 0.335, p < 0.070), *Friesea mirabilis* (r = 0.326, p < 0.079) and *Isotomiella minor* (r = 0.340, p < 0.066).

It avoids significantly sites colonized by *Mesaphorura critica* (r = -0.541, p < 0.002).

There is a tendency to avoid sites colonized by *Pseudoanurophorus alticolus*

(r = -0.327, p < 0.078). There is a weak tendency to be found at older sites (r = 0.325, p < 0.080).					
Lepidocyrtus paradoxus	**open**			**epi**	
	epigaeic (WANNER & DUNGER 2002), 1st stage of succession (DUNGER 1991), self-motile (DUNGER et al. 2002), mesophilous, macrophytobiont (RUSEK 1995), grassland (MIGLIORINI et al. 2003), under wood (FJELLBERG 1980), earliest stages in afforestation (DUNGER 1997)				
This species is significantly often found with *Folsomia fimetaria* (r = 0.499, p < 0.005), *Ceratophysella succinea* (r = 0.429, p < 0.018), *Isotomodes productus* (r = 0.369, p < 0.045), *Mesaphorura italica* (r = 0.719, p < 0.000), *Mesaphorura krausbaueri* (r = 0.463, p < 0.010), *Sminthurides malmgreni* (r = 0.719, p < 0.000), *Sminthurus viridis* (r = 0.719, p < 0.000) and *Xenylla brevicauda* (r = 0.654, p < 0.000). There is a tendency to be found with *Sphaeridia pumilis* (r = 0.339, p < 0.067) and *Tomocerus flavescens* (r = 0.341, p < 0.065). It is significantly correlated to age (r = 0.403, p < 0.027).					
Lepidocyrtus violaceus	**forest**			**epi**	
	Litter species and tree trunks (FJELLBERG 1980), woodland (STIERHOF 2003), pH 6.5 and 6.9 (ROCHEFORT et al. 2006)				
This species is significantly often found with *Arrhopalites caecus* (r = 0.665, p < 0.000), *Desoria violacea* (r = 0.401, p < 0.028), *Entomobrya corticalis* (r = 0.500, p < 0.005), *Entomobrya marginata* (r = 0.377, p < 0.040), *Folsomia penicula* (r = 0.496, p < 0.005), *Friesea mirabilis* (r = 0.419, p < 0.021), *Isotomiella minor* (r = 0.430, p < 0.018), *Lepidocyrtus cyaneus* (r = 0.391, p < 0.033), *Metaphorura affinis* (r = 0.370, p < 0.044), *Micraphorura absoloni* (r = 0.627, p < 0.000), *Protaphorura armata* (r = 0.479, p < 0.007), *Protaphorura meridiata* (r = 0.678, p < 0.000), *Orchesella flavescens* (r = 0.488, p < 0.006), *Pseudachorutes parvulus* (r = 0.500, p < 0.005) and *Xenylla grisea* (r = 0.463, p < 0.010). There is a tendency to be found with *Folsomia quadrioculata* (r = 0.341, p < 0.065), *Willemia anophthalma* (r = 0.328, p < 0.077). It is significantly positively correlated to structure (0.402, p < 0.028), organic matter content (r = 0.371, p < 0.044) and water capacity (r = 0.371, p < 0.044). There is a tendeny to be found at sites with higher conductivity (r = 0.338, p < 0.068), water content (r = 0.343, p < 0.068), ammonium (r = 0.343, p < 0.063) and nitrate (r = 0.359, p < 0.060).					
Megalothorax minimus	**forest**			**endo**	
	Euedaphic (CHAUVAT et al. 2003), parthenogenic (PETERSEN 1978), ubiquist (HAGVAR 1982, KOVÁC et al. 2001),				

	mesophilous, euedaphobiont (RUSEK 1995), forest in dune succession (SLAWSKA 1997), "late" species (PARR 1979), forest (STERZYNSKA & KUZNETSOVA 1997), pH indifferent (PONGE 2000), most advanced stages of succession, significantly correlated to soil moisture (KOVÁC et al. 2004), prefers beech over spruce forest (CASSAGNE 2004), forest (own results)

This species is significantly often found with *Anurophorus atlanticus* (r = 0.597, p < 0.000), *Desoria violacea* (r = 0.556, p < 0.001), *Entomobrya corticalis* (r = 0.670, p < 0.000), *Folsomia penicula* (r = 0.384, p < 0.036), *Folsomia quadrioculata* (r = 0.454, p < 0.012), *Friesea mirabilis* (r = 0.384, p < 0.036), *Mesaphorura yosii* (r = 1.000, p < -), *Metaphorura affinis* (r = 0.515, p < 0.004), *Micraphorura absoloni* (r = 0.526, p < 0.003), *Pseudachorutes parvulus* (r = 0.670, p < 0.000), *Pseudachorutes subcrassus* (r = 0.670, p < 0.000), *Tomocerus minor* (r = 1.000, p < -), *Vertagopus arboreus* (r = 0.420, p < 0.021), *Willemia anophthalma* (r = 0.372, p < 0.043), *Xenylla acauda* (r = 0.515, p < 0.004) and *Xenylla grisea* (r = 0.670, p < 0.000).

There is a tendency to be found with *Arrhopalites caecus* (r = 0.347, p < 0.060), and *Isotomiella minor* (r = 0.333, p < 0.072), *Orchesella cincta* (r = 0.347, p < 0.060), *Protaphorura armata* (r = 0.344, p < 0.062)

The species was not found within the successional chronosequence.

Mesaphorura atlantica	**open**	**dry**	**acidophilous**	**endo**	
	Euedaphic species known as dominant in reclaimed English coal areas (MOORE & LUXTON 1988), the Rhineland brown-coal area (SCHULZ 2003, pers. com.), early stages of succession (RUSEK 2004), dominant in earliest stages of succession in the post-mining area of Lower Lusatia and (sub)rezedent in an oak-forest in Lower Lusatia, acidophilous, pH < 5, driest and poorest sites with few vegetation (own results)				

This species is significantly often found with *Pseudoanurophorus alticolus* (r = 0.407, p < 0.026).

It significantly avoids sites colonized by *Lepidocyrtus lanuginosus* (r = -0.475, p < 0.008), *Neanura muscorum* (r = -0.454, p < 0.012) and *Parisotoma notabilis* (r = -0.556, p < 0.001).

There is a tendency to avoid sites colonized by *Entomobrya multifasciata* (r = -0.329, p < 0.079) and *Friesea mirabilis* (r = -0.344, p < 0.063).

It is significantly negatively correlated to organic matter content (r = -0.546, p < 0.002), conductivity (r = -0.533, p < 0.002), water content (r = -0.542, p < 0.002), water capacity (r = -0.441, p < 0.015) and ammonium (r = -0.545, p < 0.002).

Mesaphorura critica	**open**			**endo**	
	It is a common euedaphic species in open habitats such as arable fields, grasslands, dunes but also in forests (DUNGER 1994). Abundant in almost all successional stages in reclaimed land after lignite mining (ZERLING 1990), open habitats (KOVÁC & MIKLISOVÁ 1997), grassland (RUSEK 1989), mostly in dry meadows, rare in forests (FJELLBERG 1998), prefers pine plantations over oak woods (KOVAC et al. (2005), rarely reported from mine sites (DUNGER et al. 2004)				
It significantly avoids sites colonized by *Lepidocyrtus lanuginosus* (r = -0.369, p < 0.044), *Lepidocyrtus lignorum* (r = -0.541, p < 0.002), *Neanura muscorum* (r = -0.388, p < 0.034), *Tomocerus vulgaris* (r = -0.401, p < 0.028). There is a tendency to avoid sites colonized by *Entomobrya muscorum* (r = -0.341, p < 0.065), *Micraphorura pygmea* (r = -0.337, p < 0.068) and *Parisotoma notabilis* (r = -0.353, p < 0.056). It is significantly positively correlated to pH (r = 0.372, p < 0.043). There is a tendency to colonize sites with less developed vegetation structure (r = -0.331, p < 0.074).					
Mesaphorura hylophila	**open**		**acidintolerant**	**endo**	
	euedaphic species in different open habitats (moist and dry grasslands, fields) and forests (DUNGER 1994), abundant in almost all successional stages in reclaimed land after lignite mining (ZERLING 1990), grassland (RUSEK 1989), in rich deciduous forests, more rare in meadows and coniferous forests (FJELLBERG 1998), acido-intolerant (PONGE 2000), more advanced stages of succession (RUSEK 2004), grassland (own results)				
This species is significantly often found with *Cryptopygus thermophilus* (r =0.376, p < 0.041), *Entomobrya muscorum* (r = 0.368, p < 0.045), *Micranurida pygmea* (r = 0.387, p < 0.035), *Willemia anophthalma* (r = 0.404, p < 0.027), *Willemia aspinata* (r = 0.381, p < 0.038). There is a tendency to be found with *Mesaphorura italica* (r = 0.325, p < 0.079), *Pseudoanurophorus alticolus* (r = 0.325, p < 0.080), *Sminthurides malmgreni* (r = 0.325, p < 0.079), *Sminthurus viridis* (r = 0.325, p < 0.079). There is a tendency to avoid sites colonized by *Entomobrya lanuginosa* (r = -0.342, p < 0.065).					
Mesaphorura italica	**forest**		**acidintolerant**	**endo**	
	A hemiedaphic species, mainly in woodlands, but also in dry grasslands and				

	sandy soils (DUNGER 1994). Later in succession than *M. critica, M. hydrophila* and *M. macrochaeta* (ZERLING 1990), both in forest soils and meadows (FJELLBERG 1998), acido-intolerant (PONGE 2000)

This species is significantly often found with *Folsomia candida* (r = 0.372, p < 0.043), *Lepidocyrtus paradoxus* (r = 0.719, p < 0.000), *Sminthurides malmgreni* (r = 1.000, p -), *Sminthurus viridis* (r = 1.000, p < -), *Xenylla brevicauda* (r = 0.490, p < 0.006).

There is a tendency to be found with *Folsomia fimetaria* (r = 0.333, p < 0.072), *Mesaphorura hylophila* (r = 0.325, p < 0.079) and *Pseudoanurophorus alticolus* (r = 0.347, p < 0.060).

The species was not found within the forest chronosequence.

Mesaphorura krausbaueri	**open**	**moist**	**acidintolerant**	**endo**	
	Meadows and forest soil, often in damp habitats (FJELLBERG 1998), prefers wet and dry meadows, also in forest soils (DUNGER 1994), pH 5.2 (VAN STRAALEN & VERHOEF 1997), acido-intolerant (PONGE 2000), not in PML (DUNGER et al. 2004, own results)				

This species is significantly often found with *Ceratophysella succinea* (r = 0.998, p < 0.000), *Isotomodes productus* (r = 0.401, p < 0.028), *Lepidocyrtus paradoxus* (r = 0.463, p < 0.010) and *Tomocerus flavescens* (r = 0.370, p < 0.044).

There is a tendency to be found with *Ceratophysella denticulata* (r = 0.341, p < 0.065), *Entomobrya multifasciata* (r = 0.325, p < 0.080)

There is an almost significant tendency to be found at sites with high pH values (r = 0.358, p < 0.052).

The species was not found within the forest chronosequence.

Mesaphorura macrochaeta	**open**	**dry**		**endo**	
	Euedaphic (CHAUVAT et al. 2003) species in coniferous and deciduous woodland, acidophilious (PONGE 1993), pH indifferent (PONGE 2000), moist grasslands, urban habitats (DUNGER 1994). 1st stage of succession in reclaimed areas (ZERLING 1990, DUNGER 1994, KRAWCZYNSKI & BRÖRING 2004), for decades dominant on reclaimed site (DUNGER 1991), most abundant in dry meadows (FJELLBERG 1998), dominant under spruce in the Pyrenees (CASSAGNE et al. 2004), lawns, pH 6.5 and 6.9 (ROCHEFORT et al. 2006)				

This species is significantly often found with *Willemia anophthalma* (r = 0.408, p < 0.025).

There is a tendency to be found with *Cryptopygus thermophilus* (r =0.332, p

< 0.073) and *Willemia aspinata* (r = 0.343, p < 0.063). There is a tendency to be found at sites with organic matter content (r = 0.334, p < 0.071) and higher water content (r = 0.333, p < 0.078).					
Mesaphorura tenuisensillata	**ubiquist**		**acidophilous**	**endo**	
	Generalist (HAGVAR 1982), euedaphic (DUNGER 1991, CHAUVAT et al. 2003) species in different habitats: moist and dry grasslands, moss, forests and caves (DUNGER 1994), parthenogenic (PETERSEN 1978), wide ecological amplitude: dunes, meadows, forests (FJELLBERG 1998), acidophilic (PONGE 2000), rarely reported from mine sites (DUNGER et al. 2004)				
There is a tendency to be found with *Lepidocyrtus cyaneus* (r = 0.345, p < 0.062), *Schoetella ununguiculata* (r = 0.357, p < 0.053) and *Sphaeridia pumilis* (r = 0.339, p < 0.068).					
Mesaphorura yosii	**forest**		**acidophilous**	**endo**	
	euedaphic (HAGVAR & ABRAHAMSEN 1984, CHAUVAT et al. 2003) species in coniferous and deciduous woodland, in sandy soils and bogs (DUNGER 1994), acidophilous (≤ pH 4 HAGVAR 1995, PONGE 2000), parthenogenic (PETERSEN 1978), mostly in acid soils in coniferous forests, more rare in deciduous forests (FJELLBERG 1998), acid humus forms (PONGE et al. 2003)				
This species is significantly often found with *Anurophorus atlanticus* (r = 0.597, p < 0.000), *Desoria violacea* (r = 0.556, p < 0.001), *Entomobrya corticalis* (r = 0.670, p < 0.000), *Folsomia penicula* (r = 0.384, p < 0.036), *Folsomia quadrioculata* (r = 0.454, p < 0.012), *Friesea mirabilis* (r = 0.384, p < 0.036), *Megalothorax minimus* (r = 0.1.000, p < -), *Metaphorura affinis* (r = 0.515, p < 0.004), *Micraphorura absoloni* (r = 0.526, p < 0.003), *Orchesella cincta* (r = 0.347, p < 0.060), *Pseudachorutes parvulus* (r = 0.670, p < 0.000), *Pseudachorutes subcrassus* (r = 0.670, p < 0.000), *Tomocerus minor* (r = 1.000, p < -), *Vertagopus arboreus* (r = 0.420, p < 0.021) and *Willemia anophthalma* (r = 0.372, p < 0.043), *Xenylla acauda* (r = 0.515, 0.004) and *Xenylla grisea* (r = 0.670, p < 0.000). There is a tendency to be found with *Arrhopalites caecus* (r = 0.347, p < 0.060), *Isotomiella minor* (r = 0.333, p < 0.072), *Protaphorura armata* (r = 0.344, p < 0.062) It was not found in the successional chronosequence.					
Metaphorura affinis	**open**		**acidintolerant**	**endo**	
	open habitats (DUNGER 1994, KOVÁC & MIKLISOVÁ 1997), mesophilous, euedaphobiont (RUSEK 1995), dry beach meadows and open lowland heaths, more				

	rare in forests (FJELLBERG 1998), acido-intolerant (PONGE 2000)
This species is significantly often found with *Anurophorus atlanticus* (r = 0.624, p < 0.000), *Arrhopalites caecus* (r = 0.407, p < 0.025), *Desoria violacea* (r = 0.628, p < 0.000), *Entomobrya corticalis* (r = 0.771, p < 0.000), *Folsomia quadrioculata* (r = 0.521, p < 0.003), *Lepidocyrtus violaceus* (r = 0.370, p < 0.044), *Megalothorax minimus* (r = 0.515, p < 0.004), *Mesaphorura yosii* (r = 0.515, p < 0.004), *Micraphorura absoloni* (r = 0.518, *Protaphorura armata* (r = 0.633, p < 0.000) and *Protaphorura meridiata* (r = 0.566, p < 0.001), *Pseudachorutes parvulus* (r = 0.771, p < 0.000), *Pseudosinella octopunctata* (r = 0.369, p < 0.045) and *Tomocerus minor* (r = 0.515). There is a tendency to be found with *Folsomia penicula* (r = 0.351, p < 0.057), *Vertagopus arboreus* (r = 0.339, p < 0.066). It is significantly positively correlated to water capacity (r = 0.368, p < 0.046) and ammonium (r = 0.430, p < 0.018). There is a tendency to be found at sites with better developed vegetation structure (r = 0.340, p < 0.066), lower pH values (r = -0.328, p < 0.077) and higher organic matter content (r = 0.340, p < 0.066).	
Micranurida pygmea	**open** | **acidophilous** | **endo**
	Acidophilous (HAYBACH 1959, ≤ pH 4 HAGVAR 1995, PONGE 2000, STIERHOF 2003), 2nd stage, endogaeic (DUNGER 1989), Hemiedaphic (CHAUVAT et al. 2003), parthenogenic (PETERSEN 1978), forest (SLAWSKI & SLAWSKA 2000), hygrophil, euedaphobion (RUSEK 1995), wide variety of habitats, even dry situations like coastal sand dunes (FJELLBERG 1998), earliest forest stages (DUNGER 1997)
This species is significantly often found with *Cryptopygus thermophilus* (r =0.428, p < 0.018), *Mesaphorura hylophila* (r = 0.387, p < 0.035), *Willemia anophthalma* (r = 0.370, p < 0.044) and *Willemia aspinata* (r = 0.457, p < 0.011). There is a tendency to be found with *Gisinianus flammeolus* (r = 0.328, p < 0.076), *Micraphorura absoloni* (r = 0.326, p < 0.078) and *Xenylla grisea* (r = 0.352, p 0.056). There is a tendency to avoid sites colonized by *Entomobrya lanuginosa* (r = -0.325, p < 0.080), *Mesaphorura critica* (r = -0.337, p < 0.068) and *Sminthurus nigromaculatus* (r = -0.325, p < 0.080).	
Micraphorura absoloni	**forest** | **acidphilous** | **epi**
	parthenogenic (PETERSEN 1978), generalist (HAGVAR 1982), forest (SLAWSKI & SLAWSKA 2000), mostly in forest litter (FJELLBERG 1998), acidophilic (PONGE 2000), forest (own results)

This species is significantly often found with *Anurophorus atlanticus* (r = 0.544, p < 0.002), *Arrhopalites caecus* (r = 0.610, p < 0.000), *Desoria violacea* (r = 0.563, p < 0.001), *Entomobrya corticalis* (r = 0.703, p < 0.000), *Folsomia penicula* (r = 0.690, p < 0.000), *Folsomia quadrioculata* (r = 0.457, p < 0.011), *Friesea mirabilis* (r = 0.443, p < 0.014), *Isotomiella minor* (r = 0.605, p < 0.000), *Lepidocyrtus violaceus* (r = 0.627, p < 0.000), *Megalothorax minimus* (r = 0.526, p < 0.003), *Mesaphorura yosii* (r = 0.526, p < 0.003), *Metaphorura affinis* (r = 0.518, p < 0.003), *Orchesella flavescens* (r = 0.463, p < 0.010), *Protaphorura armata* (r = 0.467, p < 0.009), *Protaphorura meridiata* (r = 0.382, p < 0.037), *Pseudachorutes parvulus* (r = 0.703, p < 0.000), *Tomocerus minor* (r = 0.526, p < 0.003), *Willemia anophthalma* (r = 0.380, p < 0.039) and *Xenylla grisea* (r = 0.676, p < 0.000).

There is a tendency to be found with *Micranurida pygmea* (r = 0.326, p < 0.078).

It is significantly negatively correlated to *Entomobrya multifasciata* (r = -0.362, p < 0.049).

It is significantly positively correlated to water capacity (r = 0.381, p < 0.038).

It is significantly negatively correlated to pH (r = -0.476, p < 0.008).

There is a tendency to be found at sites with better developed vegetation structure (r = 0.344, p < 0.063), water content (r = 0.343, p < 0.068).

Microanurophorus musci	**open**			**endo**	
	Psammophilous species, mostly in continental sand (STERZYNSKA, pers.comment)				

This species is significantly often found with *Heteromurus nitidus* (r = 0.369, p < 0.045), *Pseudoanurophorus alticolus* (r = 0.495, p < 0.005) and *Sminthurus nigromaculatus* (r = 0.431, p < 0.017).

Neanura muscorum	**forest**			**epi**	
	Hemiedaphic (CHAUVAT et al. 2003), epigaeic forest species (DUNGER 1991, KOVÁC & MIKLISOVÁ 1997), species absent for a long time after fire, K-strategist (TAMM, 1986), forest (SLAWSKI & SLAWSKA 2000), mesophilous, xylobiont (RUSEK 1995), wide variety of habitats (FJELLBERG 1998), litter layer of preferably coniferous forests, low dominances				

This species is significantly often found with *Anurophorus atlanticus* (r = 0.401, p < 0.028), *Entomobrya lanuginosa* (r = 0.441, p < 0.015), *Folsomia dovrensis* (r = 0.384, p < 0.036), *Folsomia penicula* (r = 0.637, p < 0.000), *Friesea mirabilis* (r = 0.627, p < 0.000), *Heteromurus nitidus* (r = 0.445, p < 0.014), *Isotomiella minor* (r = 0.461, p < 0.010), *Orchesella flavescens* (r = 0.585, p < 0.001), *Parisotoma notabilis* (r = 0.363, p < 0.049), *Proisotoma minima* (r = 0.518, p < 0.003), *Proisotoma minuta* (r = 0.518, p < 0.003), *Pseudachorutes subcrassus* (r = 0.488, p < 0.006), *Xenylla acauda* (r = 0.371, p < 0.043) and *Xenylla grisea* (r = 0.534, p < 0.002).

There is a tendency to be found at sites colonized by *Vertagopus arboreus* (r = 0.360, p < 0.051), *Orchesella bifasciata* (r = 0.351, p < 0.057), *Sminthurides schoetti* (r = 0.348, p < 0.060).

It significantly avoids sites colonized by *Mesaphorura atlantica* (r = -0.475, p < 0.008), *Mesaphorura critica* (r = -0.388, p < 0.034).

It is significantly correlated to structure (r = 0.442, p < 0.014), organic matter content (r = 0.425, p < 0.019), conductivity (r = 0.413, p < 0.023), water content (r = 0.443, p < 0.016), water capacity (r = 0.381, p < 0.038) and ammonium (r = 0.521, p < 0.003).

Orchesella bifasciata	**forest**	**moist**		**epi**	
	Epedaphic (WANNER & DUNGER 2002, CHAUVAT et al. 2003), in moss, litter in damp forests (FJELLBERG 1980), prefers pine plantations over oak woods (KOVAC et al. (2005)				

This species is significantly often found with *Desoria violacea* (r = 0.382, p < 0.037), *Friesea mirabilis* (r = 0.409, p < 0.025), *Heteromurus nitidus* (r = 445, p < 0.014), *Protaphorura armata* (r = 0.421, p < 0.021), *Orchesella cincta* (r = 0.711, p < 0.000), *Orchesella flavescens* (r = 0.574, p < 0.001) and *Xenylla acauda* (r = 0.369, p < 0.045).

There is a tendency to be found with *Isotomiella minor* (r = 0.342, p < 0.064), *Neanura muscorum* (r = 0.351, p < 0.057), *Willemia anophthalma* (r = 0.356, p < 0.053).

It is significantly positively correlated to structure (r = 0.401, p < 0.028), organic matter content (r = 0.391, p < 0.033) and water capacity (r = 0.419, p < 0.021).

There is a tendency to be found at sites with higher ammonium content (r = 0.356, p < 0.054).

Orchesella cincta	**forest**			**epi**	
	forest species (KOVÁC & MIKLISOVÁ 1997, MIGLIORINI et al. 2003), atmobiont, forest (PONGE 1993), afforested dumps with summer dryness and slow decomposition, epigaeic (DUNGER 1989, WANNER & DUNGER 2002), abundant in open habitats, (DUNGER 1997), epigaeic, sandy soils (JOOSSE 1981), pH 5.7 (van STRAALEN & VERHOEF 1997), self-motile (DUNGER et al. 2002), mesophilous, epigeont (RUSEK 1995), dry sites (PONGE 1993), in forests on tree trunks (FJELLBERG 1980), pH indifferent (PONGE 2000)				

This species is significantly often found with *Desoria violacea* (r = 0.385, p < 0.036), *Entomobrya muscorum* (r = 0.486, p < 0.006) *Entomobrya nivalis* (r = 0.505, p < 0.004), *Folsomia fimetaria* (r = 0.380, p < 0.038), *Heteromurus nitidus* (r = 0.413, p < 0.023), *Lepidocyrtus lignorum* (r = 0.437, p < 0.016), *Orchesella bifasciata* (r = 0.711, p < 0.000), *Orchesella flavescens* (r =

0.379, p < 0.039), *Willemia anophthalma* (r = 0.596, p < 0.001) and *Willemia intermedia* (r = 0.393, p < 0.024).

There is a tendency to be found with *Folsomia quadrioculata* (r = 0.350, p < 0.058)*, Isotomiella minor* (r = 0.347, p < 0.060), *Lepidocyrtus lanuginosus* (r = 0.346, p < 0.061), *Megalothorax minimus* (r = 0.347, p < 0.060), *Mesaphorura yosii* (r = 0.347, p < 0.060) and *Tomocerus minor* (r = 0.347, p < 0.060).

It is significantly positively correlated to structure (r = 0.410, p < 0.024).

There is a tendency to be found at sites with higher water capacity (r = 0.328, p < 0.077).

Orchesella flavescens	**forest**			**epi**	
	40-year-old dumps with deciduos forest, epigaeic (DUNGER 1989), pH 5.6 (VAN STRAALEN & VERHOEF 1997), litter (DUNGER 1997), forest (DUNGER 1991), damp forest litter (FJELLBERG 1980), forest (own results)				

This species is significantly often found with *Anurophorus atlanticus* (r = 0.362, p < 0.049), *Arrhopalites caecus* (r = 0.398, p < 0.030), *Desoria violacea* (r = 0.546, p < 0.002), *Entomobrya corticalis* (r = 0.458, p < 0.011), *Folsomia candida* (r = 0.384, p < 0.036)*, Folsomia penicula* (r = 0.618, p < 0.000), *Folsomia quadrioculata* (r = 0.511, p < 0.004)*, Friesea mirabilis* (r = 0.620, p < 0.000), *Isotomiella minor* (r = 0.600, p < 0.000), *Lepidocyrtus violaceus* (r = 0.488, p < 0.006), *Micraphorura absoloni* (r = 0.463, p < 0.010), *Neanura muscorum* (r = 0.585, p < 0.001), *Orchesella bifasciata* (r = 0.574, p < 0.001), *Orchesella cincta* (r = 0.379, p < 0.039), *Protaphorura armata* (r = 0.549, p < 0.002), *Protaphorura meridiata* (r = 0.485, p < 0.007), *Pseudachorutes parvulus* (r = 0.458, p < 0.011), *Willemia anophthalma* (r = 0.547, p < 0.002), *Xenylla acauda* (r = 0.348, p < 0.036) and *Xenylla grisea* (r = 0.490, p < 0.006).

There is a tendency to avoid sites colonized by *Schoetella ununguiculata* (r = -0.350, p < 0.058).

It is significantly positively correlated to structure (r = 0.588, p < 0.001), organic matter content (r = 0.685, p < 0.000), conductivity (r = 0.553, p < 0.002), water content (r = 706, p < 0.000), water capacity (r = 0.703, p < 0.000), ammonium (r = 0.563, p < 0.001) and nitrate (r = 0.554, p < 0.002).

Orchesella villosa	**forest**			**epi**	
	pH 6,5 (VAN STRAALEN & VERHOEF 1997), epigaeic (WANNER & DUNGER 2002), self-motile (DUNGER et al. 2002), hygrophilous (PICHARD et al. 1989, PONGE 1993), pH indifferent (PONGE 2000), frequent in dry litter of warm forests (DUNGER 1997)				

This species is significantly often found with *Entomobrya lanuginosa* (r = 0.370, p < 0.044) and *Xenylla acauda*(r = 0.401, p < 0.028).

There is a tendency to be found with *Sminthurus nigromaculatus* (r = 0.341, p < 0.065).

There is a tendency to avoid sites colonized by *Isotoma anglicana* (r = -0.328, p < 0.076)					
Paratullbergia macdougalli	**open**			**epi**	
	Leaf litter (FJELLBERG 1998), various habitats, prefers probably moist and wet sites (DUNGER 1994), not abundant (DUNGER 1997), open habitats (own results)				
This species was significantly often found with *Isotoma viridis* (r = 0.422, p < 0.020), *Isotomodes productus* (r = 0.387, p < 0.035), *Vertagopus arboreus* (r = 0.457, p < 0.011). There is a tendency to be found with *Isotoma anglicana* (r = 0.354, p < 0.055) and *Sminthurides schoetti* (r = 0.332, p < 0.073).					
Parisotoma notabilis	**ubiquist**			**endo**	
	Eurotopic and mesophilic litter-dwelling species with high abundances, prefers moderately disturbed biotopes (DUNGER 2001), 2nd stage of succession (DUNGER 1968, ZERLING 1991, KRAWCZYNSKI & BRÖRING 2004), K-strategist (ZERLING 1990), hemiedaphic (HAGVAR 1995, CHAUVAT et al. 2003), alcalophilous (VILKAMAA & HUHTA 1986, pH ≥4 HAGVAR & ABRAHAMSEN 1984, pH 5.2 VAN STRAALEN & VERHOEF 1997, HAGVAR 1995), pH indifferent (PONGE 2000), dominant in arable soils (KOVÁC & MIKLISOVÁ 1997), epigaeic (DUNGER 1989), euedaphic (DUNGER 1991, 2004), parthenogenic (DUNGER 1991, HAGVAR 1995), ubiquist (KOVÁC et al. 2001, MIGLIORINI et al. 2003), linked with the first accumulation of organic matter (DUNGER et al. 2002), mesophilous, euedaphobiont (RUSEK 1995), eumull (PONGE et al. 2003), initial coloniser on English coal heaps (PARSONS & PARKINSON 1986), earliest forest stages (DUNGER 1997), lawns, pH 6.5 and 6.9 (ROCHEFORT et al. 2006)				
This species is significantly often found with *Cyphoderus albinus* (r 0.380, p < 0.038), *Entomobrya lanuginosa* (r = 0.440, p < 0.015), *Entomobrya nivalis* (r = 0.363, p < 0.048), *Folsomia candida* (r = 0.426, p < 0.019), *Isotoma anglicana* (r = 0.387, p < 0.035), *Isotoma viridis* (r = 0.531, p < 0.003), *Isotomodes productus* (r = 0.389, p < 0.034), *Lepidocyrtus lanuginosus* (r = 0.388, p < 0.034), *Neanura muscorum* (r = 0.363, p < 0.049), *Proisotoma minima* (r = 0.434, p < 0.017). It is significantly negatively correlated with *Mesaphorura atlantica* (r = -0.556, p < 0.001) and *Sphaeridia pumilis* (r = -0.407, p < 0.026). There is a tendency to be found with *Folsomia fimetaria* (r = 0.328, p < 0.077), *Seira domestica* (r = 0.534, p < 0.055).					

There is a tendency to avoid sites colonized by *Mesaphorura critica* (r = -0.353, p < 0.056) and *Pseudoanurophorus alticolus* (r = -0.360, p < 0.051). It is significantly positively correlated to organic matter content (r = 0.466, p < 0.009), conductivity (r = 0.546, p < 0.002), water content (r = 0.445, p < 0.015), water capacity (r = 0.378, p < 0.007), phosphate (r = 0.482, p < 0.007), ammonium (r = 0.593, p < 0.001) and nitrogen (r = 0.459, p < 0.014). There is a tendency to be found at sites with more developed vegetation structure (r = 0.355, p < 0.054).					
Proisotoma minima	**forest**		**acidophilous**	**endo**	
	mesophilous, hemiedaphobiont (RUSEK 1995), coniferous forests (FJELLBERG 1980), acid humus forms (PONGE 2000, PONGE et al. 2003), 1st stage of succession (DUNGER et al. 2002)				
This species is significantly often found with *Cyphoderus albinus* (r = 0.463, p < 0.010), *Entomobrya lanuginosa* (r = 0.369, p < 0.045), *Folsomia dovrensis* (r = 0.670, p < 0.000), *Isotoma viridis* (r = 0.403, p < 0.027), *Isotomodes productus* (r = 0.370, p < 0.044), *Neanura muscorum* (r = 0.518, p < 0.003), *Parisotoma notabilis* (r = 0.434, p < 0.017), *Pseudachorutes subcrassus* (r = 0.463, p < 0.010), *Seira domestica* (r = 0.429, p < 0.018). There is a tendency to be found at sites with higher ammonium content (r = 0.354, p < 0.055).					
Proisotoma minuta	**ubiquist**		**acidintolerant**	**endo**	
	characteristic species of pioneer stages in brown-coal open cast dumps (DUNGER 1968), 1st stage of succession, r-strategist (DUNGER 1989, ZERLING 1990), thermophilous, compost and ruderal species (DUNGER 2001), compost (KOVÁC et al. 2001), euedaphic (DUNGER 1991), mesophilous, hemiedaphobiont (RUSEK 1995), decomposing organic matter (FJELLBERG 1980), compost species (STERZYNSKA & KUZNETSOVA 1997), pH 7.2 (VAN STRAALEN & VERHOEF1997), pH > 6 (own results)				
This species is significantly often found with *Isotomodes productus* (r = 0.462, p < 0.010). There is a tendency to be found with *Cryptopygus thermophilus* (r = 0.332, p < 0.073), *Folsomia manolachei* (r = 0.328, p < 0.077) and *Isotoma viridis* (r = 0.337, p < 0.069). It is significantly positively correlated to pH (r = 0.551, p <0.002).					
Protaphorura armata	**forest**		**acidophilous**	**endo**	
	Euedaphic (CHAUVAT et al. 2003), ubiquist (KOVÁC et al. 2001), various habitats, often in rather dry sites (FJELLBERG 1998), typical for				

	coniferous forest (HAGVAR 1982), acidophilic (PONGE 2000), lawns, pH 6.5 and 6.9 (ROCHEFORT et al. 2006), dry meadow (KUZNETSOVA, in press), preferably under beech (CASSAGNE et al. 2004), dry forests (STIERHOF 2003), forest (own results)

This species is significantly often found with *Anurophorus atlanticus* (r = 0.553, p < 0.002), *Arrhopalites caecus* (r = 0.618, p < 0.000), *Desoria violacea* (r = 0.591, p < 0.001), *Entomobrya corticalis* (r = 0.536, p < 0.002), *Folsomia fimetaria* (r = 0.464, p < 0.010), *Folsomia penicula* (r = 0.390, p < 0.033), *Folsomia quadrioculata* (r = 0.512, p < 0.004), *Friesea mirabilis* (r = 0.543, p < 0.002), *Isotomiella minor* (r = 0.473, p < 0.008), *Lepidocyrtus violaceus* (r = 0.479, p < 0.007), *Megalothorax minimus* (r = 0.670, p < 0.000), *Metaphorura affinis* (r = 0.633, p < 0.000), *Micraphorura absoloni* (r = 0.467, p < 0.009), *Orchesella bifasciata* (r = 0.421, p < 0.021), *Orchesella flavescens* (r = 0.549, p < 0.002), *Pseudachorutes parvulus* (r = 0.536, p < 0.002) and *Protaphorura meridiata* (r = 0.666, p < 0.000), *Willemia anophthalma* (r = 0.480, p < 0.007) and *Xenylla grisea* (r = 0.434, p < 0.017).

There is a tendency to be found with *Megalothorax minimus* (r = 0.344, p < 0.062), *Mesaphorura yosii* (r = 0.344, p < 0.062) and *Tomocerus minor* (r = 0.344, p < 0.062).

It is significantly positively correlated to structure (r = 0.410, p < 0.024), organic matter content (r = 0.516, p < 0.004) and ammonium (r = 0.487).

There is a tendency to be found at older sites (r = 0.350. p < 0.058) and sites with higher water content (r = 0.364, p < 0.052).

Protaphorura meriadiata		**moist**		**endo**	
	Alpine species (STERZYNSKA, pers. comment), probably moist sites (own results)				

This species is significantly often found with *Anurophorus atlanticus* (r = 0.540, p < 0.002), *Arrhopalites caecus* (r = 0.401, p < 0.028), *Folsomia penicula* (r = 0.424, p < 0.019), *Folsomia quadrioculata* (r = 0.418, p < 0.021), *Lepidocyrtus violaceus* (r = 0.678, p < 0.000), *Metaphorura affinis* (r = 0.566, p < 0.001), *Micraphorura absoloni* (r = 0.382, p < 0.037), *Orchesella flavescens* (r = 0.485, p < 0.007), *Protaphorura armata* (r = 0.666, p < 0.000), *Willemia anophthalma* (r = 0.364, p < 0.048).

There is a tendency to be found with *Folsomia penicula* and *F. quadrioculata, Fiesea mirabilis* (r = 0.357, p < 0.053), *Lepidocyrtus cyaneus* (r = 0.329, p < 0.075).

It is significantly positively correlated to structure (r = 0.404, p < 0.027), organic matter content (r = 0.373, p < 0.042), water capacity (r = 0.378, p < 0.039) and ammonium (r = 0.407, p < 0.026).

Pseudachorutes parvulus	**forest**			**epi**	
	Forest (PONGE 1993), forest species (KOVÁC & MIKLISOVÁ 1997), hemiedaphic (CHAUVAT et al. 2003), species absent for a long time after fire, acidiphilous, K-strategist (TAMM 1986), under bark of dead trees (FJELLBERG 1998),				

	pH indifferent (PONGE 2000), tree-climbing (DUNGER 1997), prefers pine plantations (KOVÁC ET AL. 2005), preferably under spruce (CASSAGNE et al. 2004), rarely reported from mine sites (DUNGER et al. 2004), forest (own results)

This species is significantly often found with *Anurophorus atlanticus* (r = 0.396, p < 0.045), *Arrhopalites caecus* (r = 0.573, p < 0.001), *Desoria violacea* (r = 0.831, p < 0.000), *Entomobrya corticalis* (r = 1.000, p -), *Folsomia penicula* (r = 0.532, p < 0.002), *Folsomia quadrioculata* (r = 0.707, p < 0.000), *Friesea mirabilis* (r = 0.483, p < 0.007), *Isotomiella minor* (r = 0.462, p < 0.010) , *Lepidocyrtus violaceus* (r = 0.500, p < 0.005), *Megalothorax minimus* (r = 0.670, p < 0.000), *Mesaphorura yosii* (r = 0.670, p < 0.000), *Metaphorura affinis* (r = 0.771, p < 0.000), *Micraphorura absoloni* (r = 0.703, p < 0.000), *Orchesella flavescens* (r = 0.549, p < 0.002), *Protaphorura armata* (r = 0.536, p < 0.002), *Pseudachorutes subcrassus* (r = 0.429, p < 0.018), *Tomocerus minor* (r = 0.670, p < 0.000), *Willemia anophthalma* (r = 0.443, p < 0.014) and *Xenylla grisea* (r = 0.429, p < 0.018).

It is significantly positively correlated to structure (r = 0.432, p < 0.017), organic matter content (r = 0.416, p < 0.022), water content (r = 0.406, p < 0.029), water capacity (r = 0.416, p < 0.022) and ammonium (r = 0.433, p < 0.001).

It is significantly negatively correlated to pH (r = -0.408, p < 0.025).

Pseudachorutes subcrassus	**forest**			**epi**	
	Mesophilous, hemiedaphobiont (RUSEK 1995), forest litter (FJELLBERG 1998), rarely reported from mine sites (DUNGER et al. 2004), forests (STIERHOF 2003)				

This species is significantly often found with *Anurophorus atlanticus* (r = 0.369, p < 0.045), *Cyphoderus albinus* (r = 0.500, p < 0.005), *Entomobrya corticalis* (r = 0.429, p < 0.018), *Entomobrya lanuginosa* (r = 0.401, p < 0.028), *Folsomia dovrensis* (r = 0.719, p < 0.000), *Folsomia penicula* (r = 0.493, p < 0.006), *Friesea mirabilis* (r = 0.434, p < 0.017), *Isotomiella minor* (r = 0.376, p < 0.040), *Megalothorax minimus* (r = 0.670, p < 0.000), *Mesaphorura yosii* (r = 0.670, p < 0.000), *Neanura muscorum* (r = 0.488, p < 0.006), *Proisotoma minima* (r = 0.463, p < 0.010), *Pseudachorutes parvulus* (r = 0.429, p < 0.018), *Seira domestica* (r = 0.463, p < 0.010), *Tomocerus minor* (r = 0.670, p < 0.000), *Vertagopus arboreus* (r = 0.582, p < 0.001) and *Xenylla grisea* (r = 0.429, p < 0.018).

There is a tendency to be found with *Desoria violacea* (r = 0.341, p < 0.065) and *Sminthurus nigromaculatus* (r = 0.340, p < 0.066).

It is significantly positively correlated to ammonium (r = 0.401, p < 0.028).

There is a tendency to be found at older sites (r = 0.355, p < 0.055).

Pseudoanurophorus alticolus	**open**	**dry**	**philous**		
	Dry, open habitats with weakly developed				

	vegetation, acidophilous (own results)
This species is significantly often found with *Mesaphorura atlantica* (r = 0.407, p < 0.026), *Microanurophorus musci* (r = 0.495, p < 0.005). There is a tendency to be found with *Mesaphorura hylophila* (r = 0.325, p < 0.080), *Mesaphorura italica* (r = 0.347, p < 0.060), *Sminthurinus malmgreni* (r = 0.347, p < 0.060) and *Sminthurus viridis* (r = 0.347, p < 0.060). There is a tendency to avoid sites colonized by *Lepidocyrtus lanuginosus* (r = -0.327, p < 0.078), *Lepidocyrtus lignorum* (r = -0.327, p < 0.078), *Parisotoma notabilis* (r = -0.360, p < 0.051), *Willemia intermedia* (r = -0.327, p < 0.077). It is significantly negatively correlated to structure (r = -0.387, p < 0.035), organic matter content (r = -0.441, p < 0.015), conductivity (r = -0.511, p < 0.004), water capacity (r = -0.403, p < 0.027) and ammonium (r = -0.418, p < 0.022). There is a tendency to avoid sites with higher nitrate content (r = -0.344, p < 0.073).	
Pseudosinella alba	**open** | **acidintolerant** | **epi**
	Later stage of succession, farmland, K-strategist (ZERLING 1990), mycetophagetus (PONGE 1993), open habitats (KOVÁC et al 2001), under stones, in ant hills, debris (FJELLBERG 1980), eumull, acidointolerant (PONGE 2000, PONGE et al. 2003) , "early" species (PARR 1979), epigaeic (DUNGER et al. 2002), compost species (STERZYNSKA & KUZNETSOVA 1997), lawns, pH 6.5 and 6.9 (ROCHEFORT et al. 2006), pH indifferent, preferably under spruce in the Pyrenees (CASSAGNE et al. 2004), open habitats (own results)
This species is significantly often found with *Arrhopalites caecus* (r = 0.533, p < 0.002), *Bourletiella pruinosa* (r = 0.769, p < 0.000), *Brachystomella parvula* (r = 0.580, p < 0.001), *Folsomia fimetaria* (r = 0.416, p < 0.022) and *Isotomodes productus* (r = 0.414, p < 0.023), *Isotomurus palustris* (r = 0.449, p < 0.013) and *Tomocerus flavescens* (r = 0.405, p < 0.026). There is a tendency to prefer sites with higher conductivity (r = 0.356, p < 0.054).	
Pseudosinella octopunctata	**open** | **dry** | **epi**
	Under stone (FJELLBERG 1980), epigaeic (DUNGER et al.2002), very rare species (STERZYNSKA, pers. comment), dry open environments, epigaeic, Mediterranean shrub lands (DETSIS et al. 2000), mainly forests, rare species (STIERHOF 2003)
This species is significantly often found with *Lepidocyrtus lanuginosus* (r = 0.371, p < 0.044), *Metaphorura affinis* (r = 0.369, p < 0.045). There is a tendency to be found with *Entomobrya multifasciata* (r = 0.326, p	

< 0.079) and *Tomocerus flavescens* (r = 0.340, p < 0.066).					
Schoetella ununguiculata	**open**	**dry**		**epi**	
	afforested dumps with summer dryness and slow decomposition, epigaeic (DUNGER 1989), in forest litter, in moss on tree trunks, in meadows and litter along seashore and lake margins (FJELLBERG 1998), early stages of succession (RUSEK 2004), thermophilous and xerophilous (STIERHOF 2003), open habitats (own results)				
There is an almost significant tendency to be found with *Mesaphorura tenuisensillata* (r = 0.357, p < 0.053). This species is significantly negatively correlated to *Folsomia candida* (r = -0.381, p < 0.038). There is a tendency to avoid sites colonized by *Orchesella flavescens* (r = -0.350, p < 0.058). It is significantly negatively correlated to age (r = -0.456, p < 0.011), organic matter content (r = -0.445, p < 0.014), water content (-0.446, p < 0.015), water capacity (r = -0.482, p < 0.007) and ammonium (r = -0.415, p < 0.023).					
Seira domestica	**ubiquist**			**endo**	
	eudominant in arable soils (KOVÁC & MIKLISOVÁ 1997), thermophilous (DUNGER 1997), synanthropic species (DUNGER 1997, STERZYNSKA, pers. comment), rarely reported from mine sites (DUNGER et al. 2004)				
This species is significantly often found with *Cyphoderus albinus* (r = 0.463, p < 0.010), *Entomobrya lanuginosa* (r = 0.798, p < 0.000), *Entomobrya nivalis* (r = 0.415, p < 0.022), *Folsomia candida* (r = 0.396, p < 0.030), *Folsomia dovrensis* (r = 0.670, p < 0.000), and *Hypogastrura manubrialis* (r = 0.719, p < 0.000), *Isotoma viridis* (r = 0.403, p < 0.027), *Proisotoma minima* (r = 0.429, p < 0.018), *Pseudachorutes subcrassus* (r = 463, p < 0.010). There is a tendency to be found with *Isotoma anglicana* (r = 0.348, p < 0.060), *Isotomodes productus* (r = 0.340, p < 0.066) and *Parisotoma notabilis* (r = 0.354, p < 0.055). There is a tendency to prefer sites with a high phosphate content (r = 0.326, p < 0.079). The species was not found within the forest.					
Sminthurides malmgreni	**hygrophilous**			**epi**	
	Hygrophilous (CASSAGNAU 1961, FJELLBERG 1980), hygrophilous, neustont (RUSEK 1995)				
This species is significantly often found with *Folsomia candida* (r = 0.372, p < 0.043), *Lepidocyrtus paradoxus* (r = 0.719, p < 0.000), *Mesaphorura italica* (r = 1.000, p < -), *Sminthurus viridis* (r = 1.000, p < -) and *Xenylla grisea* (r = 0.490, p < 0.006). There is a tendency to be found with *Folsomia fimetaria* (r = 0.333, p <					

0.072), *Mesaphorura hylophila* (r = 0.325, p < 0.079) and *Pseudoanurophorus alticolus* (r = 0.347, p < 0.060).					
Sminthurides schoetti	**hygrophilous**		**acidophilous**	**epi**	
	Hygrophil (FJELLBERG 1980, DUNGER 1997, 1999, CHERNOVA & KUZNETSOVA 2000), drift exposed (DUNGER et al. 2002), open habitats, hygrophilous (STIERHOF 2003), alcalophilous, hygrophilous (own results)				
This species is significantly often found with *Anurophorus atlanticus* (r = 0.400, p < 0.028), *Arrhopalites caecus* (r = 0.458, p < 0.011), *Friesea mirabilis* (r = 0.414, p < 0.023), *Hypogastrura manubrialis* (r = 0.414, p < 0.023), *Isotoma viridis* (r = 0.418, p < 0.021), *Isotomiella minor* (r = 0.395, p < 0.031), *Isotomodes productus* (r = 0.668, p < 0.000), *Sphaeridia pumilis* (r = 0.443, p < 0.014) and *Xenylla grisea* (r = 0.534, p < 0.002). There is a tendency to be found with *Neanura muscorum* (r = 0.348, p < 0.060), *Paratullbergia macdougalli* (r = 0.332, p < 0.073), *Vertagopus arboreus* (r = 0.332, p < 0.073) and *Xenylla brevicauda* (r = 0.343, p < 0.064). It is significantly positively correlated to conductivity (r = 0.449, p < 0.013) and nitrate (r = 0.482, p < 0.009). There is a tendency to be found at sites with higher organic matter content (r = 0.355, p < 0.054).					
Sminthurinus aureus	**open**		**acidintolerant**	**epi**	
	Hemiedaphic (CHAUVAT et al. 2003), epigaeic (DUNGER 1989, STERZYNSKA & KUZNETSOVA 1997), hemiedaphic or epigaeic (DUNGER 1999), mesophilous, epigeont (RUSEK 1995), dry or mesic meadows (FJELLBERG 1980), eumull, acido-intolerant (PONGE 2000, PONGE et al. 2003), acido-intolerant, hygrophilous (own results)				
There is a tendency to be found with *Gisinianus flammeolus* (r = 0.328, p < 0.077) and *Xenylla acauda* (r = 0.349, p < 0.059). There is a tendency to avoid sites colonized by *Sminthurus nigromaculatus* (r = -0.324, p < 0.080). It is significantly positively correlated to organic matter content (r = 0.422, p < 0.020), conductivity (r = 0.514, p < 0.004) and water content (r = 0.465, p < 0.011). There is a tendency to be found at sites with higher water capacity (r = 0.351, p < 0.057).					
Sminthurus nigromaculatus	**open**	**dry**		**epi**	
	Dry grasslands (FJELLBERG 1980, DUNGER 1999), mesophilous, macrophytobiont (RUSEK 1995)				
This species is significantly often found with *Entomobrya nivalis* (r = 0.467, p					

< 0.009), *Folsomia dovrensis* (r = 0.515, p < 0.004), *Microanurophorus musci* (r = 0.431, p < 0.017) and *Vertagopus arboreus* (r = 0.388, p < 0.034).

There is a tendency to be found with *Cyphoderus albinus* (r = 0.340, p < 0.066), *Isotoma viridis* (r = 0.328, p < 0.077), *Orchesella villosa* (r = 0.341, p < 0.065) and *Pseudachorutes subcrassus* (r = 340, p < 0.066).

There is a tendency to avoid sites colonized by *Micranurida pygmea* (r = -0.325, p < 0.080) and *Sminthurinus aureus* (r = -0.324, p< 0.080).

It is significantly negatively correlated to conductivity (r = -0.372, p < 0.043).

Sminthurus viridis	**open**			**epi**	
	Meadow species (PONGE 1993), open habitats (KOVÁC & MIKLISOVÁ 1997, MIGLIORINI et al. 2003), moister grasslands (FJELLBERG 1980, DUNGER 1999), mesophilous, macrophytobiont (RUSEK 1995)				

This species is significantly often found with *Folsomia candida* (r = 0.372, p < 0.043)*, Lepidocyrtus paradoxus* (r = 0.719, p < 0.000), *Mesaphorura italica* (r = 1.000, p < -), *Sminthurides malmgreni* (r = 1.000, p < -) and *Xenylla brevicauda* (r = 0.490, p < 0.006).

There is a tendency to be found with *Folsomia fimetaria* (r = 0.333, p < 0.072), *Mesaphorura hylophila* (r = 0.325, p < 0.079), *Pseudoanurophorus alticolus* (r = 0.347, p < 0.060).

Sphaeridia pumilis	**hygrophilous**			**epi**	
	Young afforestations, epigaeic (DUNGER 1989), euedaphic (CHAUVAT et al. 2003), different moist soils (DUNGER 1999), mesophilous, epigaeic (RUSEK 1995), muscicolous (MIGLIORINI et al. 2003), hygrophilous (PONGE 1993, DUNGER 1997), lawns, pH 6.5 and 6.9 (ROCHEFORT et al. 2006)				

This species is significantly often found with *Folsomia candida* (r = 0.375, p < 0.041)*, Folsomia fimetaria* (r = 0.428, p < 0.018), *Isotoma viridis* (r = 0.419, p < 0.021), *Isotomodes productus* (r = 0.393, p < 0.032), *Parisotoma notabilis* (r = 0.407, p < 0.026), *Sminthurides schoetti* (r = 0.443, p < 0.014) and *Xenylla grisea* (r = 0.534, p < 0.002) and *Xenylla brevicauda* (r = 0.445, p < 0.014)..

There is a tendency to be found with *Arrhopalites caecus* (r = 0.333, p < 0.072), *Lepidocyrtus paradoxus* (r = 0.339, p < 0.067), *Mesaphorura tenuisensillata* (r = 0.338, p < 0.068) and *Xenylla brevicauda* (r = 0.343, p < 0.064).

It is significantly positively correlated to conductivity (r = 0.461, p < 0.010), water content (r = 0.461, p < 0.012), phosphate (r = 0.456, p < 0.011), ammonium (r = 0.390, p < 0.033) and nitrate (r = 0.405, p < 0.033).

There is a tendency to be found at sites with higher pH (r = 0.332, p < 0.073) and sites with higher organic matter content (r = 0.332, p < 0.073).

Tomocerus flavescens	**forest**		**philous**	**epi**	
	40-year-old dumps with deciduous forest, epigaeic (DUNGER 1989), litter (DUNGER 1997), species absent for a long time after fire, K-strategist (TAMM, 1986) acidophilous, pH 2.9 (VAN STRAALEN & VERHOEF 1997), damp habitats (FJELLBERG 1980), rare species (STIERHOF 2003)				
This species is significantly often found with *Arrhopalites caecus* (r = 0.406, p < 0.026), *Cyphoderus albinus* (r = 0.369, p < 0.045), *Folsomia fimetaria* (r = 0.602, p < 0.000), *Heteromurus nitidus* (r = 0.597, p < 0.000), *Isotoma viridis* (r = 0.622, p < 0.000), *Isotomurus palustris* (r = 0.366, p < 0.046), *Lepidocyrtus lanuginosus* (r = 0.470, p < 0.009), *Lepidocyrtus lignorum* (r = 0.396, p < 0.030), *Mesaphorura krausbaueri* (r = 0.370, p < 0.044), *Pseudosinella alba* (r = 0.405, p < 0.026) and *Xenylla brevicauda* (r = 0.456, p < 0.011). There is a tendency to be found with *Ceratophysella succinea* (r = 0.341, p < 0.065), *Entomobrya multifasciata* (r = 0.341, p < 0.065), *Lepidocyrtus paradoxus* (r = 0.341, p < 0.065), *Pseudosinella octopunctata* (r = 0.340, p < 0.066).					
Tomocerus minor	**hygrophilous**		**indifferent**	**epi**	
	Hygrophilous (SZEPTYCKI 1967, FJELLBERG 1980, PICHARD et al. 1989, CASSAGNE et al. 2004), pH 4.7 (VAN STRAATEN & VERHOEFF 1997), drought sensitive (PARSONS & PARKINSON 1986), pH indifferent (PONGE 2000), reported from mine sites of northern England (DUNGER et al. 2004)				
This species is significantly often found with *Anurophorus atlanticus* (r = 0.597, p < 0.000), *Desoria violacea* (r = 0.556, p < 0.001), *Entomobrya corticalis* (r = 0.670, p < 0.000), *Folsomia penicula* (r = 0.384, p < 0.036), *Folsomia quadrioculata* (r = 0.454, p < 0.012), *Friesea mirabilis* (r = 0.384, p < 0.036), *Isotomurus palustris* (r = 0.366, p < 0.046), *Megalothorax minimus* (r = 1.000, p < -), *Mesaphorura yosii* (r = 1.000, p < -), *Metaphorura affinis* (r = 0.515, p < 0.004), *Micraphorura absoloni* (r = 0.526, p < 0.003), *Pseudachorutes parvulus* (r = 0.670, p < 0.000), *Pseudachorutes subcrassus* (r = 670, p < 0.000), *Vertagopus arboreus* (r = 0420, p < 0.021), *Willemia anophthalma* (r = 0.372, p < 0.043), *Xenylla acauda* (r = 0.515, p < 0.004) and *Xenylla grisea* (r = 0.670, p < 0.000). There is a tendency to be found with *Arrhopalites caecus* (r = 0.347, p < 0.060), *Isotomiella minor* (r = 0.333 p < 0.072), *Orchesella cincta* (r = 0.347, p < 0.060) and *Protaphorura armata* (r = 0.344, p < 0.062).					
Tomocerus vulgaris	**open**			**epi**	
	epigaeic (DUNGER 1989), open habitats (DUNGER 1991), dry litter (DUNGER 1997), later stage of succession after fire, open habitats (TAMM 1986), littoral, swamps, mesophilous, epigaeic (RUSEK 1995)				

There is a tendency to be found with *Isotomurus palustris* (r = 0.344, p < 0.062).

It significantly avoids sites colonized by *Mesaphorura critica* (r = -0.401, p < 0.028).

Vertagopus arboreus	**forest**	**dry**		**endo**	
	Dry forest (PONGE 1993), corticolous, rare, forests, deficient ecological knowledge (STIERHOF 2003), forests and clearings (own results)				

This species is significantly often found with *Anurophorus atlanticus* (r = 0.594, p < 0.001), *Folsomia dovrensis* (r = 0.391, p < 0.033)*, Megalothorax minimus* (r = 0.420, p < 0.021) and *Mesaphorura yosii* (r = 0.420, p < 0.021), *Metaphorura affinis* (r = 0.339, p < 0.066), *Paratullbergia macdougalli* (r = 0.457, p < 0.011), *Pseudachorutes subcrassus* (r = 582, p < 0.001), *Sminthurus nigromaculatus* (r = 0.388, p < 0.034), *Tomocerus minor* (r = 0.420, p < 0.021) and *Xenylla grisea* (r = 0.518, p < 0.003).

There is a tendency to be found with *Friesea mirabilis* (r = 0.358, p < 0.052), *Neanura muscorum* (r = 0.360, p < 0.051), *Sminthurides schoetti* (r = 0.332, p < 0.073) and *Xenylla acauda* (r = 0.325, p < 0.080).

It is significantly positively correlated to structure (r = 0.418, p < 0.021).

Willemia anophthalma	**ubiquist**		**philous**	**endo**	
	Euedaphic (CHAUVAT et al. 2003), acidophilious (GISIN 1943, HAYBACH 1959, VILKAMAA & HUTHA 1986, PARSONS & PARKINSON 1986, ≤ pH 4 HAGVAR & ABRAHAMSEN 1984, PONGE 1993, PONGE 2000), mycetophagetus (PONGE 1993), mesophil, euedaphobiont (RUSEK 1995), characteristic for coniferous forests (SZEPTYCKI 1967), common in meadows and forest litter (FJELLBERG 1998), ubiquist (HAGVAR 1982), acid humus forms (PONGE et al. 2003), prefers beech over spruce (CASSAGNE et al. 2004), correlated to organic matter and *Willemia aspinata* but different dominances, acidophilic forest species (STIERHOF 2003), forest (own results)				

This species is significantly often found with *Desoria violacea* (r = 0.542, p < 0.002), *Entomobrya corticalis* (r = 0.443, p < 0.014), *Entomobrya muscorum* (r = 0.636, p < 0.000), *Entomobrya nivalis* (r = 0.434, p < 0.016), *Folsomia candida* (r = 0.365, p < 0.047)*, Folsomia fimetaria* (r = 0.401, p < 0.028), *Folsomia quadrioculata* (r = 0.498, p < 0.005)*, Isotomiella minor* (r = 0.438, p < 0.015), *Megalothorax minimus* (r = 0.372, p < 0.043), *Mesaphorura hylophila* (r = 0.404, p < 0.027), *Mesaphorura macrochaeta* (r = 0.408, p < 0.025), *Mesaphorura yosii* (r = 0.372, p < 0.043), *Micraphorura absoloni* (r = 0.380, p < 0.039), *Micranurida pygmea* (r = 0.370, p < 0.044), *Orchesella cincta* (r = 0.596, p < 0.001), *Orchesella flavescens* (r = 0.547, p < 0.002),

Protaphorura armata (r = 0.480, p < 0.007), *Protaphorura meriadiata* (r = 0.364, p < 0.048), *Pseudachorutes parvulus* (r = 0.443, p < 0.014), *Tomocerus minor* (r = 0.372, p < 0.043) and *Xenylla grisea* (r = 0.412, p < 0.024).

There is a tendency to be found with *Folsomia penicula* (r = 0.352, p < 0.056), *Gisinianus flammeolus* (r = 0.345, p < 0.062), *Lepidocyrtus lanuginosus* (r = 0.357, p < 0.053), *Lepidocyrtus violaceus* (r = 0.328, p < 0.077), *Orchesella bifasciata* (r = 0.356, p < 0.053) and *Protaphorura armata*.

It is significantly positively correlated to structure (r = 0.577, p < 0.001), organic matter content (r = 0.490, p < 0.006), water content (r = 0.588, p < 0.001), water capacity (r = 0.572, p < 0.001) and ammonium (r = 0.575, p < 0.001).

There is a significant negative correlation to pH (r = -0.461, p < 0.010).

Willemia aspinata	**forest**			**endo**	
	Coniferous litter (FJELLBERG 1980), acidophilous, coniferous forests, cool, humid climate (STIERHOF 2003)				

This species is significantly often found with *Cryptopygus thermophilus* (r = 0.395, p < 0.031), *Gisinianus flammeolus* (r = 0.719, p < 0.000), *Mesaphorura hylophila* (r = 0.381, p < 0.038), *Mesaphorura macrochaeta* (r = 0.343, p < 0.063) and *Micranurida pygmea* (r = 0.457, p < 0.011).

There is a tendency to be found with *Entomobrya muscorum* (r = 0.340, p < 0.066) and *Mesaphorura macrochaeta* (r = 0.343, p < 0.063).

Willemia intermedia	**open**		**philous**	**endo**	
	Later stage of Succession, K-strategist (ZERLING 1990), mycetophagetus (PONGE 1993), euedaphic (DUNGER 1991), in Scandinavia dry alpine meadows, sandy seashore meadows (FJELLBERG 1998), acidophilic (PONGE 2000), dry, lime-rich soils (DUNGER 1997)				

It is significantly often found with *Orchesella cincta* (r = 0.393, p < 0.032)

There is a tendency to be found with *Entomobrya muscorum* (r = 0.333, p < 0.073).

There is a tendency to avoid sites colonized by *Pseudoanurophorus alticolus* (r = -0.327, p < 0.077).

Xenylla acauda	**open**	**dry**		**epi**	
	Sandy beach meadows in Scandinavia (FJELLBERG 1998)				

This species is significantly often found with *Folsomia quadrioculata* (r = 0.456, p < 0.011)*, Friesea mirabilis* (r = 0.370, p < 0.044), *Megalothorax minimus* (r = 0.515, p < 0.004), *Mesaphorura yosii* (r = 0.515, p < 0.004), *Neanura muscorum* (r = 0.372, p < 0.043), *Orchesella bifasciata* (r = 0.369, p < 0.045), *Orchesella flavescens* (r = 0.384, p < 0.036), *Orchesella villosa* (r = 0.401, p < 0.028) and *Tomocerus minor* (r = 0.515, p < 0.004).

There is a tendency to be found with *Sminthurinus aureus* (r = 0.349, p< 0.059) and *Vertagopus arboreus* (r = 0.325, p < 0.080).

It is significantly correlated to structure (r = 0.375, p < 0.041).

Xenylla brevicauda	**forest**	**dry**		**epi**	
	Forest litter, mainly coniferous (FJELLBERG 1998), dry sites (RUSEK 1992), rare species, coniferous forests (STIERHOF 2003)				

This species is significantly often found with *Arrhopalites caecus* (r = 0.621, p < 0.000), *Brachystomella parvula* (r = 0.407, p < 0.026), *Entomobrya corticalis* (r = 0.429, p < 0.018), *Folsomia fimetaria* (r = 0.419, p < 0.021), *Lepidocyrtus paradoxus* (r = 0.654, p < 0.000), *Lepidocyrtus violaceus* (r = 0.463, p < 0.010), *Mesaphorura italica* (r = 0.490, p < 0.006), *Sminthurides malmgreni* (r = 0.490, p < 0.006), *Sminthurus viridis* (r = 0.490, p < 0.006), *Sphaeridia pumilis* (r = 0.445, p < 0.014) and *Tomocerus flavescens* (r = 0.456, p < 0.011).

There is a tendency to be found with *Sminthurides schoetti* (r = 0.343, p < 0.064) and *Xenylla grisea* (r = 0.341, p < 0.065).

Xenylla grisea	**forest**		**acidintolerant**	**epi**	
	Typical for xeric sites (KUBIKOVA & RUSEK 1976), forest (SCHLEUTER 1984), under bark and in forest litter (FJELLBERG 1998), acido-intolerant (PONGE 2000), rarely reported from mine sites (DUNGER et al. 2004), warmer climate (STIERHOF 2003)				

This species is significantly often found with *Anurophorus atlanticus* (r = 0.829, p < 0.000), *Arrhopalites caecus* (r = 0.597, p < 0.000), *Entomobrya marginata* (r = 0.402, p < 0.028), *Folsomia fimetaria* (r = 0.419, p < 0.021), *Folsomia penicula* (r = 0.513, p < 0.004), *Friesea mirabilis* (r = 0.483, p < 0.007), *Isotomiella minor* (r = 0.445, p < 0.014), *Lepidocyrtus violaceus* (r = 0.463, p < 0.010), *Megalothorax minimus* (r = 0.670, p < 0.000), *Mesaphorura yosii* (r = 0.670, p < 0.000), *Micraphorura absoloni* (r = 0.676, p < 0.000), *Neanura muscorum* (r = 0.534, p < 0.002), *Orchesella flavescens* (r = 0.490, p < 0.006), *Protaphorura armata* (r = 0.434, p < 0.017), *Pseudachorutes parvulus* (r = 0.429, p < 0.018), *Pseudachorutes subcrassus* (r = 429, p < 0.018), *Sminthurides schoetti* (r = 0.534, p < 0.002), *Tomocerus minor* (r = 0.670, p < 0.000), *Vertagopus arboreus* (r = 0.518, p < 0.003) and *Willemia anophthalma* (r = 0.412, p < 0.024).

There is a tendency to be found with *Desoria violacea* (r = 0.341, p < 0.065), *Micranurida pygmea* (r = 0.352, p < 0.056) and *Xenylla brevicauda* (r = 0.341, p < 0.065).

There is a tendency to avoid sites colonized by *Isotoma anglicana* (r = -0.328, p < 0.076).

It is significantly positively correlated to structure (r = 0.416, p < 0.022), organic matter content (r = 0.400, p < 0.029) and water capacity (r = 0.400, p < 0.029).

It is significantly negatively correlated to pH (r = -0.432, p < 0.017).

Overview of study sites

Table 44: Overview of study sites and soil parameters.

site name	pH	loss on ignition (%)	conductivity (µs/cm)	water content (%)	water capacity (%)	phosphate (mg/100g)	ammonium (µg/g)	nitrate (µg/g)
alt-oak-100	2,9	29,02	82,10	35,61	93,42	0,36	0,73	0,61
alt-oak-29	2,9	21,39	115,92	27,44	85,58	0,40	0,41	0,96
alt-oak-44	3,2	23,31	99,57	35,12	86,21	0,38	0,81	0,78
cot-den-13	6,5	5,21	95,68	16,54	43,76	1,36	0,22	0,19
cot-spa-4	7,3	1,08	58,03	2,53	23,56	0,37	0,07	0,10
dom-pin-37	4,8	24,03	128,53	39,18	89,40	0,91	0,31	2,43
koy-bar-54	4,0	7,24	37,59	11,92	36,73	0,05	0,24	0,16
koy-den-54	3,8	7,61	59,82	27,28	58,25	2,27	0,55	0,80
koy-oak-24	3,9	4,62	47,92	15,08	47,75	0,38	0,29	0,56
koy-oak-34	3,4	11,18	62,56	29,95	64,77	0,82	0,48	0,33
ple-bar-59	4,5	0,77	8,47	2,97	26,88	0,87	0,07	-
ple-den-59	4,7	3,56	33,22	10,59	37,03	1,05	0,56	0,37
ple-oak-43	5,6	14,35	59,32	17,66	53,43	0,92	0,44	0,33
ple-pin-20	4,8	2,43	20,94	6,47	33,45	0,89	0,14	-
sch-bar-4	3,5	1,53	28,23	5,75	23,26	0,09	0,12	0,34
sch-den-16	7,2	8,00	80,43	17,32	27,49	0,08	0,27	0,40
sch-den-23	7,5	10,45	158,33	33,05	61,43	1,74	0,33	1,85
sch-den-29	4,7	3,71	26,21	10,21	42,82	0,67	0,34	0,51
sch-den-5	6,3	1,72	47,03	-	31,66	2,22	0,24	0,24
sch-den-8	7,0	2,33	101,67	16,53	30,76	0,99	0,53	0,72
sch-den-ref1	5,4	2,49	29,23	11,22	41,17	1,20	0,34	0,57
sch-den-ref2	7,6	18,89	107,83	14,33	47,01	1,08	0,26	0,52
sch-oak-23	4,4	5,11	27,95	6,68	33,61	0,95	0,17	0,42
sch-pin-16	5,4	1,60	27,80	6,64	28,92	0,65	0,09	0,30
sch-pin-23	3,8	3,35	68,00	10,79	41,67	0,16	0,20	0,64
sch-spa-16	7,4	1,80	60,13	6,52	46,41	0,11	0,12	0,44
sch-spa-19	4,5	1,51	23,69	7,11	32,63	0,32	0,09	0,37
sch-spa-29	6,1	1,51	17,50	3,39	30,03	0,73	0,06	0,19
sch-spa-29.1	4,2	1,84	30,12	5,03	31,89	0,14	0,28	0,57
sch-spa-ref	4,3	1,85	15,03	15,03	28,29	0,47	0,08	0,12

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